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THE BOTANICAL REVIEW

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THE PHYTOGEOGRAPHY OF UNGLACIATED EASTERN UNITED STATES AND ITS INTERPRETATION

E. LUCY BRAUN [2]

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INTRODUCTION

Unglaciated eastern United States is here interpreted as including the area south of the limits of continental ice sheets and east of the 98th meridian, i.e., the forest area in contrast to the grassland. The Driftless Area of southwestern Wisconsin and adjacent Illinois, Iowa and Minnesota, and the small unglaciated spots in eastern Canada are not included, except as their features may help to explain problems in the area under consideration.

[1] The spellings "Southern Appalachians" and "southern Appalachians" have been retained in this article in order to emphasize specificity in the case of the former; and the forms "peneplain" and "peneplane", "relic" and "relict" have been retained in deference to the authors cited.

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The literature of floristic plant geography for the most part deals with isolated species or groups of species, or with the features of limited areas differing vegetationally and floristically from the prevailing types. The unusual, rather than the usual, has attracted attention, and often proves of great value in reconstructing past events. The only more or less comprehensive treatment is included in Harshberger's "Phytogeographic Survey of North America" (112). Here, in addition to depicting regional vegetation through descriptions (with floristic lists) of specific local areas, Harshberger includes theoretic considerations dealing with the geologic evolution of floras, the history of floras and the affinities displayed. His map (p. 206), illustrating centers of plant dispersal determined by glaciation, long remained the embodiment of current ideas. More recent investigations have changed the details, although some of the basic ideas remain. Many of the floristic districts which he located and characterized are still recognized. His statements concerning affinities of North American floras do not depart greatly from present-day beliefs, although some of his examples cannot now be used, and some of his geologic interpretations must be revised.

Two principal divisions of unglaciated eastern United States may be recognized: (*a*) an older upland area which includes the Appalachian Highlands and Interior Low Plateau to the east of the Mississippi River, and the Interior Highlands (Ozark and Ouachita provinces) to the west of the Mississippi River; (*b*) the younger coastal plain area. The dominant vegetation of the older area is deciduous forest, made up largely of species belonging to genera of wide distribution in temperate latitudes; coniferous communities are more or less local. In the younger area, deciduous forest communities and their associated species are more circumscribed, while evergreen species, both needle-leaf and broad-leaf, assume prominence, and a tropical or subtropical element is conspicuous in the flora. In both of these areas, local communities, apparently not in accord with the regional vegetation, occur. Disjunct occurrence of species is frequent—of upland species in the coastal plain area, of coastal plain species in the upland. Such extraneous species often give clues to past events. Endemics, some local, some approaching "wides" in the extent of their ranges, are numerous on the Coastal Plain and in

the Appalachian Highlands, less numerous but present in the Interior Low Plateau and the Interior Highlands.

The existing pattern of distribution is a result of present and past conditions of the environment. Edaphic factors play an important role in determining local distribution. Topographic factors, through their influence on soils and soil moisture, and on local atmospheric factors, are also important. They determine, in large part, the microclimates of an area, in contrast to the regional climate. But topography changes, and consequently, through geologic time, the physiography of large areas gradually changes in accord with the progress of the erosion cycle. One type of habitat will decrease in extent, while another increases. Species ranges must shift with such environmental changes, or ecotypes develop which are suited to certain microclimates of the changed area. Climate determines potential range, within the limits set by local factors. But climates have changed in the past, and therefore the ranges of species or whole groups of species—communities—change; enforced migrations take place. Migration often results in disjunction of range; in isolation of relatively small units of the population of a species; in gradual change in morphologic characters of a species from one part to another of its changing range; in contacts between related species formerly entirely distinct in range but capable of hybridizing when they come in contact.

Disjunction—brought about by advancing migration—may result when dispersal and changing conditions permit establishment in a new location. It may result, also, when changing conditions allow influx of new and different populations which crowd out the former occupants or surround them where they remain in isolated colonies. Disjunction of the latter kind is more frequent. Such disjunction of range may be brought about when previously continuous habitats—edaphic, topographic, or climatic—are disrupted by topographic processes or by change in continental configuration or climate. Persistence of disjuncts depends on fitness of the local environment, and often, in addition, on lessened competition due to the unsuitable character of the local environment for the regional vegetation type. The compensating effects of the local environment may overcome the unfavorable character of the regional environment.

Isolation, brought about by disjunction, may result in the evolution of distinct varieties or even species. Ordinarily, this is evident only after a long period of separation, but in some instances, changes are rapid.

Because most species are variable and composed of a number of biotypes having slightly different tolerances, changing conditions and migration may result in partial segregation of variants which are arranged along a gradient from one extreme to another. Or, changing conditions may result in the destruction of biotypes and ecotypes, resulting in reduction of range of formerly widespread species. Further depletion of biotypes may result because of isolation of small populations (183). On the other hand, hybridization is made possible either by the break-down of ecologic barriers (usually by modified conditions) or by contacts brought about by shifting populations and reduction of extent of barriers during climatic and physiographic changes. Thus came about the hybridization of species of *Iris* in the Mississippi delta (8, 202) and in the interior where ranges were modified by glaciation (7); in *Tradescantia* (7, 8); in *Vaccinium* (43); in fact, in many genera. Repeated back-crossing sometimes tends to obscure the hybrid nature of resulting forms; it results in the "gradual infiltration of the germplasm of one species into that of another"—introgressive hybridization. As Anderson (9) points out, "all the widespread eastern species which have so far been analysed exhibit introgression along the Ozark-Texas axis, if they have a related taxon in that direction".

The interpretation of existing phytogeography must be based on evidence gleaned from a number of unlike sources: from the distribution pattern itself, the relationship of species and communities, their geographic extent or degree of continuity or disjunction; from the correlation between distribution and physiographic and climatic history; from the physical features of the environment, which alone or in part may explain existing distribution; from hybrids and population variation; and from fossils. Obviously, this leads us into a number of diverse fields—floristics, involving modern taxonomy and genetics, synecology, pedology (including permafrost features), climatology, physiography and paleontology.

Much of the information of significance for phytogeographic

studies is hidden in a mass of irrelevant material. Statements here and there, often without correlation with distribution, will add to the sum total of knowledge bearing on past migrations and present distribution. A search for all of these in the literature of the diverse fields of science relevant to our topic is not possible; yet some references of this sort will be given in order to emphasize the expanding future of phytogeographic studies. A number of publications treat plant geography in its broad aspects, or emphasize the underlying principles and related topics; chief among these are books by Cain (38), Good (96) and Wulff (218).

FLORISTICS

Interest in the floristics of eastern North America was first aroused by Asa Gray, who more than a century ago (97) pointed out the remarkable resemblance between the floras of eastern America and eastern Asia, and offered the then remarkable suggestion that " the extant vegetable kingdom has a long and eventful history, and that the explanation of apparent anomalies in the geographic distribution of species may be found in the various and prolonged climatic or other physical vicissitudes to which they have been subject in earlier times;—that the occurrence of certain species, formerly supposed to be peculiar to North America, in a remote or antipodal region affords of itself no presumption that they originated there ". In a series of later papers (162) Gray continued to make comparison between American and other floras, and to point out special features of our flora. Decades later the problem of relationships of floras, of specific segregations and identities, gained renewed prominence because of Fernald's publications (83, 84).

In plant geography it has been more or less customary to refer to the " elements " of a flora, and to " floristic affinities " and relationships. " Element " has been used in a variety of ways, frequently in combination with a defining adjective, as northern element, Appalachian element, Tertiary element, endemic element, relic element, etc. Although attempts have been made to confine its use to the geographic sense, the more acceptable usage is a broad one (38, 218). Affinities refer to the elements displayed by and relationships of the flora of a natural area; and sometimes, more artificially, to the flora of a political unit, as a state.

Throughout the East the Tertiary element is prominent. This is the so-called Arcto-Tertiary flora.

A considerable number of genera of the Arcto-Tertiary flora are circumboreal in distribution; others are restricted to eastern America and eastern Asia; a few are confined to one continent. They are generally conceded to be restricted remnants of the widespread mesophytic mid-Tertiary floras whose genera date from Cretaceous or early Tertiary time. Evolution through the millions of years following separation, restriction of range and ultimate isolation has indeed been slow, for differences between the species of genera of eastern American-eastern Asian or eastern American-European distribution are sometimes slight.

The term "Arcto-Tertiary" was introduced as "Arctic-Tertiary" by Engler to designate the flora of the Arctic in Tertiary time, a flora similar to that of our temperate latitudes today. However, as Wulff (218) points out, this was not an arctic flora, and the term may therefore be misleading. It was a temperate flora, and the warmer-climate Tertiary flora of slightly lower latitudes (called "boreal-Tertiary" by Engler) was a warm-temperate or subtropical flora. Li (123) suggests that the term "Tertiaro-mesophytic" be used for this element of our flora. However, there seems to be little reason to displace the established term. Arcto-Tertiary may be defined as the flora which "had its wide development at high northern latitudes" and which "lived in a region of summer rainfall and winter cold, as judged by the habits of related living trees" (52). The Arcto-Tertiary flora "may be subdivided into typically temperate and boreal units" (50).

Some of the eastern American species of the typically temperate Arcto-Tertiary flora belong to genera of circumboreal range (e.g., *Salix, Quercus, Betula*); some are circumscribed in range (most of our so-called Tertiary or Miocene relics); and some belong to genera of eastern American–eastern Asian distribution but are widely distributed in eastern America. Genera with examples of widely distributed American species are *Liriodendron,* with one closely related species of restricted range in Asia; *Sassafras,* with two Asiatic species of somewhat limited range; *Magnolia,* with wides in both hemispheres; *Epigaea,* whose one Asiatic species is rather limited in range; and *Stylophorum,* with medium ranges in

both America and Asia. Ranges of the American species of the last two examples, as well as of many other species, are in part determined by edaphic factors; *Stylophorum* is generally confined to rich woods on calcareous soils; *Epigaea* to a somewhat drier type of woods on non-calcareous soils. In these cases geographic distribution of calcareous rock influences the range of species, both of which illustrate the American-Asian disjunction, and both of which must have had comparable geologic history. Both of these, also, may be used as examples to illustrate the importance of environmental factors in limiting present species ranges, of "historical factors" in accounting for presence and persistence to the present time, when local environment becomes operative in determining precise range. Mason (126, 127) would place more emphasis on the local environmental factors of the present, and objects to the phrase "historical factor", although he does concede that "the history of a plant species may tell the very important story of *how* it arrived in any given place and *where* it came from".

EXTRA-CONTINENTAL RELATIONSHIPS

The eastern American–eastern Asian and American-European or American-Eurasian relationships are most pronounced in the floras of the upland (older) areas of eastern United States; the tropical affinities, in the flora of the Coastal Plain. The latter, on the whole, are more remote. A North American–South American relationship is evident in a few plant families; this is well illustrated by the huckleberries (42).

The American-Asian and American-European relationships involve many instances of close specific relationship and even of specific identity. A considerable number of common genera have representatives in America, Europe and Asia (as *Fagus, Acer, Castanea, Populus*), species for the most part of the holarctic flora. Some are confined to America (sometimes both east and west) and southeast Europe and/or nearby southwestern Asia (as *Platanus, Cercis*), or are in these two places and eastern Asia (as *Liquidambar*). Other genera are restricted to eastern America and eastern Asia. Some of these (as *Carya*) are better represented in America; others (as *Magnolia* and *Astilbe*) in Asia; still others have only two or three species in the two areas

(as *Liriodendron, Sassafras, Stylophorum, Shortia*). Most of the species originally thought of as identical are no longer so considered; some, instead, are thought of as closely related pairs of species, or in a few instances as varieties of a single species. Almost 25 years ago Fernald (84) pointed out "that in nearly all groups the species of the Western Hemisphere are completely segregated from those of the eastern; that we have stable or essentially stable specific entities". As examples of pairs of closely related species are *Liriodendron tulipifera* of eastern America and *L. chinense* of central China, limited in distribution and not discovered until 1873 (123); *Gymnocladus dioica* of America and *G. chinensis* of central China. As examples of the varietal relationship may be cited *Circaea quadrisulcata* of Asia and its variety *canadensis* of eastern America; *Ranunculus gmelini* and its two American varieties; *Polygonum sagittatum* of eastern America and its Asiatic varieties (101, 102). As may be expected, there are sometimes differences of opinion as to the status of taxa, as to whether certain taxa are specifically distinct or are only varieties of a single species—for example, *Tovara virginiana* (86, 123, 176) and *Mitchella repens,* whose Asiatic representative is sometimes considered only a variety (123). In some cases the resemblance between the American and Asiatic species is superficial, and the relationship is generic only. On the other hand, no varietal differences can be discerned in *Symplocarpus foetidus, Caltha palustris* and *Monotropa uniflora.*

The change in viewpoint concerning specific identity in no way lessens the importance of the real problem, one of startling relationship between remote areas.

The greatest concentration of plants of restricted range which display the eastern American–eastern Asian affinity is in the southern part of the Appalachian Highlands, particularly in the southern section of the Blue Ridge province, including the Great Smoky Mountains, the Blue Ridge and the many shorter more or less transverse ranges of the area. Here, too, are endemic representatives of genera of wider distribution, but genera whose maximum development is in the Southern Appalachians and mountains of Asia, e.g., *Rhododendron.*

Probably most of the better known examples of plants with Old World relatives are those mentioned by Fernald, as the American

species of *Shortia, Buckleya, Diphylleia, Stewartia* and *Neviusia* among the local endemics, and of *Liriodendron, Cladrastis, Hamamelis, Sassafras* and many others among the endemics of wider range (83, 84). He points out that "In the ancient Appalachian Upland of the United States the outstanding phytogeographic feature is . . . the great mesophytic forest of Mesozoic or early Cenozoic genera, many of them formerly found likewise in Europe, western America and the Arctic but now restricted to one or more areas of eastern North America, eastern, central or southwestern Asia or the geologically ancient peninsulas of southeastern Europe".

Of all the local endemics, *Shortia galacifolia* has received most attention because of its interesting history of discovery and rediscovery. First found by André Michaux in 1788, it was not—in spite of Asa Gray's diligent search—rediscovered until 1879. Since then it has been located in a number of places in the mountainous area where North Carolina, South Carolina and Georgia come together, i.e., in the headwaters of the Keowee River and in the tributaries of the Catawba River about 70 miles to the northeast (38, 65, 72, 115, 116). It grows on steep banks in the shelter of *Rhododendron, Kalmia, Magnolia,* hemlock and white pine, where such ground-cover evergreens as *Asarum virginicum, Galax aphylla* and *Mitchella repens* occur. All three species of *Shortia* (*S. galacifolia* and the two Asiatic species) are very local mountain plants. All are considered Tertiary relics representing restricted remnants of a former wide distribution of ancestral forms. That former wide range [3] was modified, disrupted and curtailed by events of Tertiary time. As all known stations are within 15 miles of the divide between Atlantic and Gulf drainage, it is safe to assume that all are within the area of the residual mountain mass which rose above the peneplain produced in Miocene time; and that to this mountain haven the ancient population of *Shortia* became restricted. Deep ravines with slopes affording suitable habitat must have been present in this area continuously since early Tertiary time and throughout the time of maximum extent

[3] Such "wide range" does not imply continuous range in space; it implies, rather, continuous in time but shifting in space, or sometimes splitting and diverging from a former ancestral site. It is used in much the same way as "past range" shown by fossils, which may, usually does, represent different horizons.

of the peneplain. Uplift and subsequent erosion have deepened the valleys and doubtless have resulted in shifts in positions occupied by *Shortia*. Recently, comparison of specimens from the Keowee and from the Catawba drainage has disclosed "distinct floral variations", on the basis of which plants from the sources of the Catawba River have been designated as var. *brevistyla* Davies (65). As the rate of evolution in *Shortia* has been very slow (American and Asian species separated for geologic ages), varietal segregation can be considered as indicative of a long period of separation of the populations of *S. galacifolia*. The geographic separation, although apparently not great, assumes a different light in view of a peculiarity of seed reproduction. The seeds germinate within the ovary; then the stem decays and falls over (38, 159). As *Shortia* grows in dense mats, the chance of survival of seedlings so produced is small; only stems at the margin of a patch would have much chance of coming in contact with the soil. Migration would be infinitely slow. This interesting plant can endure temperatures far lower than those experienced in its native habitat; it has been grown successfully in New Hampshire where temperatures of –40° F. are recorded, and in Quebec, 15 miles north of Montreal (116). Its lack of an effective dispersal mechanism and its hardiness should be considered in connection with persistence of "Miocene relics" in the Southern Appalachians throughout the cold phases of the Pleistocene.

No other Appalachian endemics have received the attention that has been given to *Shortia*. Yet there are other rare species and many of more or less localized distribution which are mentioned in the literature (29, 32, 33, 34, 38, 41, 84, 110, 112, 123, 162). *Diphylleia cymosa*, of rich moist soil in the cove hardwood forests, and *Buckleya distichophylla*, parasitic on the roots of hemlock, are localized in the Southern Blue Ridge province; *Rhododendron catawbiense*, *Stewartia ovata* (*pentagyna*), *Astilbe biternata* and *Clethra acuminata* occur both in the mountains and along the rugged western border of the Appalachian Plateau, but are absent from the intervening area where the Schooley peneplain was best developed. *Galax aphylla*, the only species of its genus but with related genera in Asia, has a comparable but somewhat wider distribution, including a number of outlying stations, some of which are on the Coastal Plain (see discussion of diploid and tetraploid races).

Some of the American representatives of genera of eastern American–eastern Asian relationship have their centers of distribution west of the Appalachian Highlands. *Cladrastis lutea,* most abundant in the Interior Low Plateau of Kentucky, and with disjunct occurrence in the Ozarks of southwestern Missouri and in the Southern Appalachians, is very closely related to *C. shikokiana* of Japan (123). *Cladrastis* is known to have been present in America in early Tertiary time (22, 25, 33).

A lesser number of species display relationship with southeastern Europe, or with southeastern Europe and adjacent Asia. The genera of woody plants (as *Cercis, Platanus*) are usually ones of more southern distribution than many of the holarctic genera. Pairs of species (vicariads) showing an American-European relationship are for the most part found among herbaceous plants (38, 83). Examples are *Hepatica americana* and *H. nobilis* (*triloba*), *Anemone quinquefolia* and *A. nemorosa,* which Fernald (83) says " are obviously related though perfectly distinct species and it is clear that they have long been geographically isolated ". *Oxalis montana* and *O. acetosella,* distinguished as species by Fernald (86), are not separated by Hara (102) and only doubtfully so by Gleason (95).

The fossil record discloses that many of the genera now confined to America and Asia had representatives in Europe in pre-Pleistocene time (maps, 23), that Tertiary ranges included America, Europe and Asia. The widespread Tertiary ranges were interrupted by continental change (the breaking of land connections) and later curtailed by Pleistocene glaciation which killed out the European representatives of many genera. Within the continents physiographic changes correlated with erosion cycles brought about areal changes in vegetation, involving migration of species. Those of mountainous habitats were necessarily restricted to areas always mountainous. Thus the concentration of species of eastern American–eastern Asian relationship in the Southern Appalachians is explained.

The younger coastal plain area is strikingly different in vegetation and floristics from the older upland area. Although many of the more widespread species of eastern American–eastern Asian genera are present, many of the characteristic members of the flora of the Coastal Plain belong in " groups with wide tropical and subtropical range, the families, tribes, genera and sections

shared by the Americas with tropical and subtropical Africa, tropical and subtropical Asia, and Australia"(84). Examples are *Lachnanthes tinctoria* of the chiefly southern hemisphere Haemodoraceae; *Xyris,* a genus chiefly of the tropics and southern hemisphere. This should not be interpreted as meaning that no distinctive coastal plain species of American-Asian genera occur; some are present, as *Stewartia malacodendron,* belonging to a genus of eight species, two American (*S. ovata* of the Appalachian upland, and *S. malacodendron*) and six Asiatic (three in Japan, one in Korea, and two in central and eastern China) (123), and a family chiefly tropical in distribution (46, fig. 25; 95). *Croomia,* represented on the Gulf Coastal Plain by a local endemic (*C. pauciflora*), has two species in central and southern Japan (123). The endemic American genus, *Taxodium,* with *T. distichum* almost throughout the Coastal Plain in suitable habitats, has a long geologic record which shows that it once had Asiatic and European relatives, and that in early Tertiary time it was widespread in high latitudes (23).

The Coastal Plain, although relatively young geologically, nevertheless is the abode of many species of ancient lineage; of some, like bald cypress, whose past history is written in the fossil record; of some, like *Croomia,* whose past history is inferred from present distribution of relic species; of some, like *Stewartia malacodendron,* which may have been derived from ancient ancestors with tropical or southern hemisphere distribution and later became American-Asian in distribution; of some, like certain species of *Gaylussacia,* which seem definitely to be derived from South American relatives (see "Contributing Fields"); and of others, like *Lachnanthes,* whose relatives are chiefly tropical.

CONTINENTAL RELATIONSHIPS

In considering continental relationships it is necessary to recognize the principal physiographic areas of eastern United States, particularly the ancient Appalachian and Ozarkian uplands, and the Coastal Plain. Almost all papers dealing with floristic elements are concerned with one or more of these areas.

The flora of the ancient upland areas displays affinities with the floras of other sections of the American continent, especially with the Coastal Plain and the mountains of Mexico and Guatemala,

and to a lesser extent with the Tropics, the West and the North. The flora of the Coastal Plain, although with predominantly extra-continental affinities, contains floristic elements in common with the Appalachian and/or Ozark upland and in some cases the intervening Interior Low Plateau, and with the Great Lakes region. Disjunct distribution of species, of varieties or of related species or sections of genera illustrates the several types of geographic relationships.

UPLAND–COASTAL PLAIN AFFINITIES. The Appalachian–Coastal Plain relationship was recognized at least 75 years ago, when Redfield (156) pointed out the surprising resemblance of the flora of Table Rock, N. C., to that of the New Jersey Pine Barrens. Later, Harshberger (112) elaborated somewhat on this idea and mentioned *Hudsonia montana* on Table Rock, related to *Hudsonia tomentosa* of the Coastal Plain and northern interior, and a number of plants of the high southern mountains which also occur on the Coastal Plain. The Appalachian–Coastal Plain relationship was further stressed by Fernald (84) who pointed out that the relic colonies on the ancient and now uplifted peneplain contained plants of two categories: those belonging to tropical or austral genera (as *Lygodium, Xyris, Lobelia*), and those belonging to characteristic American endemic genera of the Coastal Plain (as *Orontium, Cleistes, Sarracenia, Hudsonia, Leiophyllum*). Later, this relationship was shown to be well displayed by relic species and colonies on the Cumberland Plateau, where extensive remnants of the Schooley peneplain afford a variety of habitats—swampy flats and depressions, and sandy flats or knolls—persisting from the ancient low-lying surface (29, 30, 32, 33). Bryophyte constituents of the coastal plain colonies of the plateau also illustrate the same sort of disjunction (167, 168, 171).

Disjunction of species range is illustrated by distribution maps of certain members of the Scrophulariaceae, as *Gratiola brevifolia, Tragiola* (*Gratiola*) *pilosa* (143); of *Cleistes* (*Pogonia*) *divaricata, Orontium aquaticum* (30); of *Uniola laxa, Panicum longifolium* (113); and by numerous floristic lists and by statements of range in manuals (29, 30, 33, 38, 86, 95, 171). In some cases the disjunct pattern is more complex, and forms, varieties or related species are involved. Examples are *Schwalbea australis* and *americana,* both of which are included in *S. americana* by Fernald

and by Gleason in the new manuals but are mapped separately by Pennell (143); *Habenaria blephariglottis,* with var. *blephariglottis* widespread and northern, var. *conspicua* in southeastern swamps and pine-barrens, and var. *integrilabia* in the relic coastal plain swamp communities of the Cumberland Plateau and on the Coastal Plain of Alabama and Mississippi (60, 86); *Leiophyllum lyoni* and *L. buxifolium* (41); *Sarracenia oreophila,* Appalachian relative of *S. flava; Sarracenia purpurea* var. *venosa,* with Appalachian stations in the Blue Ridge of North Carolina, and more extensive range across the Piedmont onto the Coastal Plain with separated areas on the Gulf slope and in New Jersey, in which latter area the widespread northern var. *purpurea* (*gibbosa*) arose (19, 207, 208, 209). A very rare and local endemic shrub of the western margin of the Cumberland (Appalachian) Plateau, *Conradina verticillata* (28), is very distinct from the other three species of the genus which are Floridian and Gulf Coast plants, a feature suggesting a long period of isolation.

In a study of North American pitcher-plants, Wherry (209) has mapped the ranges of all species and has shown by broken lines and arrows his interpretation of location of ancient stock and direction of migration to establish present range. All are interpreted as migrating from the ancient upland area as the Coastal Plain became available, or as being derived from ancient species of that upland. One species, *S. jonesii,* still inhabits a small disjunct area in the highland.

Pennell (143) has interpreted ranges of many species of the Scrophulariaceae as showing migration from ancient Appalachian upland populations; such interpretations are based on the presence of primitive characters. Of course not all species which occur on old and young land areas are so interpreted; he maintains that some have gone in one direction, some in the other.

It is rather generally agreed that the Appalachian–Coastal Plain relationship is in part a result of extensive peneplanation in Tertiary time (or Cretaceous, according to some authors), which favored the expansion of vegetation suited to a plain of low relief with swampy flats and depressions and intervening flat to rolling sandy soil areas (the underlying rock of a considerable fraction of the upland is sandstone). That is, what is now thought of as coastal plain vegetation occupied the peneplain. Uplift, with con-

sequent gradual dissection of the surface, curtailed the extent of suitable habitat on the old surface, while contemporaneously, gradual emergence of a coastal plain afforded comparable habitats which in part were populated by migration or spread from the old land area. Continued dissection so greatly reduced the remnant areas of peneplain that disjunction of the plant population resulted. The small remnants of coastal plain vegetation (relic colonies), the disjunct occurrence of species and the rare endemics reflect this past history (33, 38, 84). Cain believes that this " really is a question not of coastal plain plants in the Appalachian and Cumberland uplands, but of upland plants in the coastal plain, if we view the relationship historically ". It is also suggested that cooling, resulting from uplift and later from Pleistocene ice advances, was a factor influencing migration of tender species to the Coastal Plain. The " Hypothesis of Pleistocene origin of existing distributions " would interpret these coastal plain plants of the upland as recent (post-glacial) migrants.

The above type of distribution is one in which characteristic and often widespread coastal plain species occur as disjuncts on the upland. The reverse pattern is also seen, that of upland (inland and Appalachian) species in local areas of the Coastal Plain. This is particularly true of the hilly areas in northern Florida and adjacent Georgia (Tallahassee Red Hills, Marianna Red Lands, Apalachicola River bluffs, Eocene Red Hills, etc.), and the Tunica Hills of Louisiana, where in rich woods of ravines, many species which are not ordinarily seen on the Coastal Plain occur along with species limited to the Coastal Plain (35, 198). Local endemics, some of them very rare and local, occur along with the inland species (see section on endemics), as do also varieties and subspecies (or more rarely species) related to Appalachian or Appalachian and Ozarkian species (as of *Asclepias*, 216, 217). The widespread inland or Appalachian species are sometimes referred to as " northern disjuncts " (121, 122). The inland species which reach their southern limits in Louisiana (for the most part not mountain species as stated by Brown (35) from Cocks (54) are believed by Brown to have persisted since early Wisconsin time because of favorable topography. This hypothesis will not account for the local endemics nor the disjuncts of exacting edaphic requirements. These all indicate a more ancient refugium. It

has been suggested that the rare relic endemics, and other species perhaps derived from such relics, are " remnants of a widespread, mesic Tertiary vegetation which found refuge in northern Florida during periods of climatic stress " (198). Persistence since Tertiary time of the inland disjuncts on the Coastal Plain, together with the accompanying endemics, was made possible by the physiographic history of the areas (33). It is entirely possible, as Thorne suggests, that southward migrations of inland plants have been favored during the Pleistocene, thus augmenting the flora of the older relic communities.

The flora of the Ozark upland, like that of the Appalachian upland, has many representatives of ancient genera, a few of which are endemics or species of peculiarly disjunct range. Two of the endemics, *Castanea ozarkensis* and *Hamamelis vernalis,* have eastern as well as Asiatic relations; one, *Andrachne phyllanthoides,* is of tropical ancestry. A number of species of Appalachian or wide distribution east of the Mississippi River occur in the Ozark upland as disjuncts (33).

Coastal plain species also are present. Natural ponds, known as " sink-hole ponds ", occur on dry oak-hickory ridges and level uplands of the Ozarks of southern Missouri, and afford suitable habitat for coastal plain plants. Careful search of these areas during the past decade has resulted in discovery of a number of species not hitherto known to occur in the Ozark area (189, 190, 192, 194, 195). Although the number of such species is small—as would be expected because of the drier climate—the explanation commonly offered is the same as for coastal plain relics of the Appalachian upland. " These plants probably constitute one of the oldest recognizable elements in the present plant life of the region, harking back to conditions that prevailed before its last elevation in late Tertiary time " (140).

EASTERN UNITED STATES–MEXICAN AND –TROPICAL. Many of the genera of the ancient upland areas belong to families which include tropical and subtropical species. This is true of *Stewartia,* already mentioned as illustrating the eastern American–eastern Asian relationship. It is equally true of some of the commonest genera, as *Smilax* and *Viola.* Such relationships, however, are remote and indicate a long period of evolution from more primitive forms whose descendants are now localized in tropical or southern hemisphere latitudes to the more specialized forms of our area (46).

Closer relationships, comparable in nature to the relationships exhibited by American-European or American-Asiastic vicariads, may be found in the mountains of Mexico and Guatemala. There, in areas of older rock formations (in contrast to the younger coastal plain deposits and Pleistocene and Recent volcanic deposits), are found species common to eastern United States, varieties of our species, and also species closely related to those of eastern United States (134, 170, 191). The most conspicuous examples of identical species are trees. *Liquidambar styraciflua,* which at its lower altitudinal limits is associated with such tropical forms as tree ferns, at higher altitudes with oaks and such other eastern American species as *Carpinus caroliniana* and *Ostrya virginiana* as well as many subtropical species, some of which belong to familiar genera, is found in more of the stations studied along the eastern Escarpment of the Central Plateau and mountains of Guatemala than any other of the many identical species listed by Miranda and Sharp (134). As examples of closely related species, may be cited *Fagus mexicana,* similar to beech in southeastern United States; *Magnolia dealbata,* similar to *M. macrophylla; Sambucus mexicana,* similar to *S. canadensis; Tilia longipes,* similar to *T. heterophylla.* Some species, listed as identical, are not always so considered (181). Varietal status is given to some taxa, for example, *Ilex vomitoria* var. *chiapensis* (173).

Comparable examples of relationships could be cited from ferns, mosses and fungi (166, 169, 172). Sharp considers that "many if not most of these so-called tropical bryophytes [of eastern Tennessee] are representative of a once widespread Tertiary flora".

The family relationships are explained by Camp (46) as due to early origin of angiosperms, probably on southern hemisphere land masses, and "divergences of the basic, generalized familial groups . . . on this southern land mass certainly by the mid-Mesozoic". He points out that "the great bulk of the angiospermous families (at least their woody members) and many of their present-day genera, appear to have evolved by the Cretaceous". He believes that present distribution patterns point to the southern land masses as centers of primary evolution and centers of dispersal of evolving floras. Such an explanation means early occupancy of geologically old areas, with much more recent migration onto younger areas.

Miranda and Sharp (134) and later Sharp (174) point out the relation of the Eocene Wilcox flora of the Mississippi Embayment to the Mexican flora which contains, not only many of the Wilcox genera still known in southeastern United States, but also a considerable percentage of its more tropical genera. This implies the establishment of the vegetation of the Eastern Escarpment as resulting from southward shift of Eocene floras and perpetuation in these old land masses. Disjunction is attributed to the xeric nature of northern Mexico and southern Texas. Steyermark (191) emphasizes the importance of the geologically old mountain areas of Guatemala, not only as refuges for disjunct species of southeastern United States but also as the site of endemic species. He states that " the element of the flora of the eastern portion of the United States that reached Guatemala may have invaded that country at the end of the Cretaceous or early Tertiary when both regions were low-lying and peneplained, and previous to later uplifts ".

The many paired species and the more or less distinct varieties indicate a long period of separation—not so long, perhaps, as the American-Asiatic separation, for specific segregation is not so pronounced. It should be noted that none of the restricted species of the Southern Appalachians occurs in Mexico or Guatemala, that all the identical species are wide-ranging and that the United States representatives of paired species also are wide-ranging. Local endemics of those Latin American areas belong to genera unknown in temperate latitudes of America. They date far back in evolutionary history.

Basing conclusions on geologic features (163), Sharp (177) states that " the present temperate element in the flora of Mexico must have come from the north during late Pliocene and the Pleistocene " because, prior to the extensive faulting and volcanic activity of that time, much of Mexico was low-lying and unsuitable for temperate vegetation since the Cretaceous. In a recent analysis of floristic relationships between Mexico and the United States (71*a*), the suggestion is made that " the eastern North American plants . . . probably did not migrate southward into Mexico and Guatemala until the early Pleistocene ".

This hypothesis of late arrival of the temperate element is opposed to that based on the distribution of certain phylads which show a V-pattern and which have been explained (133) as due to

northeastward and northwestward migration from southern Mexico and Central America (see Contributing Fields). Although the eastern Cordillera and Central Plateau of Mexico are of relatively recent origin regarding elevation, it is entirely possible that the western Cordillera and land westward of the present coast of Mexico which has been down-faulted relatively recently was of sufficient elevation for the ancestral population of the temperate genera of Mexico. Migrations may have taken place both northward and southward.

It seems probable that a final separation or disjunction of the ranges of mesophytes would have been effected by the climatic barrier—a dry belt—which developed in the Pliocene. There is no evidence of opportunity for free interchange between the Mexican highlands and southeastern United States since the development of the grasslands in Pliocene time. Pluvial periods of the Pleistocene allowed "mesophytic elements in northern Mexico and Texas to meet their eastern relatives", as shown by introgression in *Juniperus* (9, 99) and *Cercis* (9). However, such xero-mesophytes as *Juniperus* and *Cercis* are not comparable in moisture requirements to the disjunct mesophytes of the mountains of Mexico and Guatemala. The "warm-moist" interval in post-Pleistocene time indicated by the pollen profile of a Texas bog (150) permitted *Castanea* to extend a hundred miles beyond its present limit (at the same time that grasses and oaks were abundant); but does not seem to have been favorable to any appreciable proportion of mesophytes.

EASTERN UNITED STATES AND THE WEST. All authors treating the vegetation or floristics of the prairie States point out the western and the eastern elements in the flora. Such dovetailing of floras, well illustrated in Kansas (93), North Dakota (160), Missouri (140), Oklahoma and Texas, ordinarily does not involve pronounced disjunction and therefore will not be considered here. Relic prairie species and prairie colonies in the eastern deciduous forest are disjuncts commonly interpreted as a result of the post-Wisconsin "xerothermic period". This phytogeographic feature will be considered in sections on prairie relics and persistence near the glacial border.

Disjunct identical species and closely related species of eastern United States and the far West are relatively few. *Polypodium*

vulgare, of Europe and western America, and *P. virginianum*, sometimes considered to be only a variety, illustrate a peculiar distribution pattern of closely related taxa (81, 83, 95). Ranges given in the manuals (86, 95) enable one to find examples of species of eastern range which also occur in California and/or other Pacific Coast states. Sharp (175) lists some of these when pointing out "relationships between the floras of California and southeastern United States". Examples of identical species are *Agrimonia grypsosepala* and *Ranunculus pusillus;* of pairs of closely related species, *Dirca palustris* and *D. occidentalis*, *Pachistima canbyi* and *P. myrsinites* (in both cases, the only two species of their respective genera). The western species of *Dirca* is very local—restricted to an area 90 by 12 miles in the Oakland and Berkeley hills (183); the eastern species of *Pachistima* is local. McVaugh suggests that these very similar (or identical?) "species" of *Dirca* migrated long ago from an ancestral area in Mexico, that their distribution pattern is referable to the V-form shared by many phylads (133).

This East-West disjunction is explained by Sharp as attributable to the bisection of formerly continuous ranges, in the north by Pleistocene glaciation, in the center and south by a xerothermic period or periods, or by earlier events. In the case of such distinct specific segregation as displayed by the two species of *Pachistima*, the separation would seem to date back to late Tertiary time, if not earlier. *Pachistima* is an ancient genus, its presence in eastern United States dating back to the Ripley flora and late Cretaceous time (24). The peculiar disjunct range of the eastern *P. canbyi* (31, 128) also suggests the influence of events earlier than Pleistocene, as most of its stations are in the old (Tertiary) Teays drainage.

A few of the endemics of the Appalachian shale barrens have western relatives, as do also those of the granite flat rocks of the Southeast (see section on endemics). The rather distant relationship of eastern and western species of *Ranunculus* (see "Contributing fields of botany") is said to date back to Tertiary time (20).

A number of species common to eastern and western forests (as *Viola canadensis*) are not disjuncts, but have a continuous range in a great northern arc around the interior grassland.

EASTERN UNITED STATES AND THE NORTH. The mountain ranges of eastern United States extend in a southerly direction

from the cooler latitudes of the Northeast. Hence the ranges of many species which are rather wide in the north extend southward along the mountains at increasing elevations as lower latitudes are reached. Many do not have even approximately continuous ranges in the mountains but instead appear here and there as disjuncts. The latter group is usually of greater interest to the plant geographer. A few examples of paired or vicarious species also fall within this general distribution pattern, as *Abies balsamea* and *A. fraseri, Diervilla lonicera* and *D. sessilifolia.* Outside of the mountains, which afford a climatic environment similar to that of more northern latitudes, some northern disjuncts occur as well as some with more or less continuous ranges but more abundant northward.

The spruce-fir forest of high elevations of the Southern Appalachians has been shown to be " distinct yet a part of the boreal forest formation " . Although it contains a number of species in common with the more northern forest, it has in all layers species not occurring in the North (139). However, the " northern affinity " is apparent in both physiognomy and floristic composition (37, 139).

Disjunct occurrence of northern species at elevations of the Southern Appalachians below the spruce-fir forest (37) and at widely separated localities throughout much of unglaciated eastern United States except the Coastal Plain (the " northern disjuncts " of hilly areas of the Coastal Plain are species widespread in the deciduous forest belt) has been noted by many authors (5, 17, 29, 33, 62, 71, 140, 143, 166, 167, 186, 192). Some of these note only occurrence and offer no interpretation; for example, *Betula papyrifera* on North Fork Mountain in West Virginia (5), *Spiraea latifolia* var. *septentrionalis* on Hawksbill Mountain, Page Co., Va. (17). Some relate the outlying southern occurrences of northern species to southward migration in the Pleistocene; for example, the isolated plant of *Taxus canadensis* in the Piedmont Province in Virginia is interpreted as " a likely relict from the Pleistocene " (71); the several species more or less isolated south of the glacial boundary in Missouri are considered to have migrated southward during the " Ice-age " and to have persisted in suitable habitats (140, 192). Others suggest the possibility of greater age; for example, in his monograph on the Scrophulariaceae, Pennell (143) states, concerning *Collinsia verna,* that " the range of the

species is very largely in glaciated territory, and it may be that such remote occurrences [more southern] . . . are relicts of a preglacial more southern distribution", and of *Mimulus ringens,* that "this species, surviving glaciation presumably in the southern Appalachian upland, has so successfully reoccupied glaciated territory as to have its main present development thereon". Woodson (217) interprets the range of *Asclepias exaltata,* which is predominantly within the glaciated territory, in like manner. He says that "being preadapted to the moist woods, meadows and copses of the northeast, *A. exaltata* has proceeded to migrate into them from its ancient refugium in the southern Appalachians".

Tsuga canadensis, sometimes referred to as a northern species, is better thought of as an ancient Appalachian species, dating back to Tertiary time in the unreduced Southern Appalachians where its root parasite, *Buckleya distichophylla,* occurs (33, pp. 45, 481). Southern occurrences of *Pinus strobus* may well be explained in the same manner, as indeed may similar ranges of other species, even though such evidence as exists for *Tsuga* is not available. Neither hemlock nor white pine occurs at increasing elevations southward, as do the more distinctly northern species. Even at its southern limit in Alabama, hemlock is at a low altitude (106, 109, 165). Furthermore, hemlock is susceptible to frost damage. In an investigation of frost pockets in the High Plateau of western Pennsylvania (Kane Experimental Forest) it was found that hemlock was damaged "to a much greater degree than any of the hardwoods" and that 49 per cent of 291 hemlocks tallied in 1936 "showed evidence of past frost injury to terminal or side shoots" (114).

The occurrence of northern species of bryophytes in east Tennessee has been explained (166) as due to pre- or inter-glacial persistence. Later (167) it was suggested that "aggressive northern species not previously existing in the Southern Appalachians may have migrated southward and subsequently met one of three fates: (*a*) they may have later retreated northward, leaving no record in the south; (*b*) they may now have a continuous range to the north; (*c*) they may still be restricted or endemic in these mountains". Steere (186) discusses the disjunct distribution of *Bryoxiphium,* pointing out the "similarity between the distribution of this species and that of many preglacial and interglacial relic

species of vascular plants"; he considers it an old species, a member of a once widespread flora.

It is apparent that there are two unlike interpretations of disjunct southern occurrence of now northern species: (*a*) that such species were in the north, moved south at times of advancing ice, then moved north again, leaving part of the population in isolated suitable habitats; (*b*) that such species were widespread in preglacial or interglacial time, their ranges curtailed or in some cases bisected by advancing ice sheets, and that some failed to move northward in postglacial time while others migrated into the glaciated territory. It seems probable that the first explanation fits some cases, the second explanation others, and that each species must be considered separately. (See also section on persistence near the glacial border.)

LOCAL FLORAS

In the foregoing classification of floristic affinities, by emphasizing the larger geographic areas of unglaciated eastern United States, papers concerned with relationships displayed by more or less local floras have been slighted.

The consideration of affinities of local floras was fostered by papers by Adams (2, 3) and by Kearney (117, 118) around the turn of the century, by some of Fernald's older papers, and by Cowles' lectures on geographic botany. A large proportion of such papers deal with floras in the glaciated area (for example, 80, 130, 142); some with borderline areas (141, 160, 197); a few with parts of unglaciated eastern United States (29, 37, 85, 122, 188). The general plan of treatment varies but little. Some classify the species as intraneous or extraneous, subdividing the latter into disjunct species and species at margin of range, and ally these with definite floristic areas or with floras to the north, the south, the east, and the west; i.e., they distinguish the various "elements" or "affinities" of the flora. Fernald, for example, classifies the species of the "inner Coastal Plain of Virginia" which are "restricted in occurrence" into 17 categories illustrating affinities with other geographic areas (85). Others are concerned with only one extraneous element, thus emphasizing a specific type of distribution (142).

Certain objections to what is termed a "synthetic approach"

in the analysis of local faunas and floras are stated by Deevey (66). However, the sort of conclusions he ascribes to data derived from "analyzable species"—such as the local area in question being a part of a larger region because the majority of its species "come from" that area—seem not to have been made in most botanical papers. Cain (40) defends the classification of floristic elements in the flora of a local area at the same time that he points out certain drawbacks.

PRAIRIE RELICS

From the time of the early settlers, mention has been made of prairie and prairie inclusions (often called "barrens") within the forested region of eastern United States. The prairies of the Mississippi Valley, even the more or less disjunct prairies of the eastern part of the "Prairie Peninsula", that lobe of prairie extending eastward into Ohio, seem much less out of place than do the more southern outliers; they are in equilibrium with the climate, and in contact with bordering oak or oak-hickory forest (200). The prairies in unglaciated southern Ohio (26), in the northern district of the "Cliff Section" and in the "Knobs" east of the Bluegrass section of Kentucky are isolated prairie inclusions surrounded by more mesic forest types (33). In the Black Belt of Alabama and in Mississippi, prairie extends far eastward of the Mississippi River (33, 104, 107, 108, 124). The Barrens of western Kentucky form a great semi-circular arc following for the most part an area underlain by cavernous limestone and with poorly defined surface drainage (33, 129).

In floristic composition these prairie communities of unglaciated eastern United States resemble the prairies of the Prairie Region, but have in addition, a number of southern and Ozarkian xerophytes. They are, apparently, disjunct communities made up in large part of species displaying more or less pronounced disjunction of range. Thus in Alabama some of these prairie plants "are not found elsewhere in Alabama" (108). *Arenaria stricta* ssp. *texana* is an extreme disjunct in southern Ohio (27). Steyermark (193) separates the glabrous-leaved form of *Silphium terebinthinaceum* of these relic prairies as a distinct variety. Anderson (9) notes introgression of the Texan *Cercis reniformis* into *C. canadensis* as far east as southern Indiana and Ohio, where dwarf redbuds are frequent in prairie communities.

As some of the prairies located not far south of the glacial border may have resulted in part from migrations earlier than the post-Wisconsin " xerothermic period ", their further consideration is included in the next section of this paper. At the time that Gleason (94) outlined the probable vegetational history of the Middle West, the southern Ohio prairies that give evidence of influx from the southwest were unknown, and he thought that prairie had never encroached upon this area.

The post-Wisconsin eastward expansion of prairie is correlated with the time of the thermal maximum, the " xerothermic period ", which has been amply reviewed by Sears (164).

PERSISTENCE NEAR THE GLACIAL BORDER

The floristics of the glacial border presents problems unlike those of other areas. Often there is a motley assortment of " elements "—northern species, southern species, prairie species, local disjuncts, and endemics—assembled in localized areas and sometimes closely associated. Termination of range, not at the glacial border where there may be a distinct break in edaphic environment, but some miles south of it where no such break occurs, is a common phenomenon in the Middle West. Isolated occurrences of southern species near the border, and occurrence of southern species whose more or less continuous ranges stop 15–20 miles south of the glacial border while still abundant; disjunct occurrence in places clearly related to the preglacial or early interglacial topography; and border occurrences with stations neither to the south nor within the glaciated area—all are readily observable distribution features.

These features are usually interpreted as due to persistence of species or groups of species which entered during climatic phases of Pleistocene and Recent time unlike the present and which now remain as relic species or in relic communities, and of species which were part of the older pre-Wisconsin or preglacial vegetation (27, 33, 34, 201, 213, 214). The " Glacial Border " symposium of the Ecological Society reviews many of these features (73).

Among the early advocates of persistence not far south of the glacial border were Adams (2), Transeau (199) and Harshberger (111, 112), all of whom believed that the conifer forest belt along the ice margin west of the Appalachians was very narrow. Harshberger thought that " the glaciers did not effect the true

distribution at any great distance from the ice front" and that conifers occupied "the outer rim of tree vegetation during the glacial period". The mixed forest "south of the arctic tundra vegetation, was a remnant of the great Tertiary forest" which "persisted during the period of refrigeration with its greatest denseness in the region drained by the Tennessee River and its tributaries" and whose northeastern tongue extended well up into southeastern Pennsylvania, while "in the Ohio Valley, the streams flowing from the south during the glacial period would aid in preserving the broad-leaved mesophytes, as far north, as the Ohio River". Gleason's idea (94) was quite comparable, for, with reference to the five floristic groups of plants of the Middle West which lay outside the margin of Wisconsin ice (the prairie flora, the Ozarkian forests, the coastal plain flora, the deciduous forests of the Appalachians, and the northeastern coniferous forest), he states that "there is no reason to believe that the general space relation of these five groups has ever been altered, although they must have suffered many fluctuations in their distribution and extent during the preceding glacial advances". He considered that the coniferous forest was "reduced to a narrow strip between the ice margin and the deciduous forest". These expressions of opinion dealt with vegetation.

Basing conclusions on pollen profiles in bogs within the area of the Early Wisconsin drift and in the southern fringe of the Late Wisconsin drift, where a pronounced spruce-fir maximum persisted for a long time, Potzger (147) believes that in the Ohio-Indiana-Illinois area there are indications of "a wide belt of conifers south of the glacial border, which broadleaved species had not replaced before advance of the ice sheet known as Late Wisconsin"; and that the presence of pollens of these trees in a Texas bog was further indication of such a band.

Termination of range of species near a glacial boundary, and persistence of plants in suitable habitats in remnants of their former ranges are beliefs early fostered by Gleason (94) and Fernald (82).[4] "If a considerable number of species are now confined to an area immediately beyond a moraine and seldom occur within

[4] Fernald's discussion is so well known and has been so often reviewed that it needs no further mention here, particularly as it treats of areas beyond the range of the present review.

it", three explanations may be offered: (*a*) "present conditions of soil and climate may exclude them"; (*b*) "their migration up to the present time may have extended merely to the moraine, which they will later cross"; (*c*) "they occupied this area before or during the formation of the moraine, have occupied it ever since, and are not at present extending their range". After weighing the first two in the light of field observation, Gleason accepted the third explanation, not alone for distributions along the front of the last, but of earlier glaciations as well, and in support of which he mentioned a number of southern species whose ranges terminate in southern Illinois, although a strip of similar habitats extends northward up the Mississippi. Of course the first explanation fits many species, but when climate and edaphic factors are similar on both sides of the line, it must be ruled out. The second will fit some species, "but it is difficult to understand why the boundary of the range of numerous species should be so nicely adjusted to the moraine". There are many species, both plant and animal, whose ranges are thus nicely adjusted, as distribution maps will show (34, 196).

Persistence does not always involve termination of range; in many instances the site is notably disjunct, or local endemics are involved. Such is the case in the Driftless Area, of which Fassett (74) writes: "This distinct relic flora, practically confined to The Driftless Area, with several endemics, having its affinities in unglaciated areas to the westward or to the southeastward, may be clearly interpreted on the basis of lack of glaciation in southwestern Wisconsin". The species of *Sullivantia* are among the best of examples used to illustrate persistence. Four of the six species are in the Rocky Mountains; *S. sullivantii* (*S. ohionis*) occurs locally near the glacial border in Indiana and Ohio, with one Kentucky station, while the related *S. renifolia* is a species of the Driftless Area and occurs in two places in east-central Missouri just outside the glacial boundary—which here is the boundary of old drifts, Kansan and Illinoian (26, 27, 33, 34, 74, 192, 214). The apparent explanation is early disjunction of range of ancestral stock followed probably by migration of the separated parts, and evolution of the isolated races. Disjunction of range of *S. renifolia* appears to be an event of Illinoian or even an earlier time. The peculiar habitat (with "grotto microclimate") of this

species and *S. sullivantii* would certainly favor survival near the glacial border. *Dodecatheon meadia* var. *frenchii,* which has a range comparable to that of *Sullivantia renifolia,* occurs " in the Driftless Area and extreme southern Illinois, seeming to be a relic of a preglacial expansion of *D. Meadia*" (78). It also occurs in Kentucky, in the same area as *Sullivantia* and other disjuncts. The moss, *Bryoxiphium norvegicum,* is an old species, " undoubtedly a member of a once widespread flora which extended over the northern hemisphere in late Cretaceous or early Tertiary times ", and whose range was disrupted by glaciation, leaving relic stations in Iceland, Greenland, Washington, the Driftless Area, along and south of the Wisconsin glacial border from Missouri to Pennsylvania (186). Many decided disjuncts and peculiar assemblages of species occur in parts of the ancient Teays drainage system in Ohio and northeastern Kentucky, and have been interpreted as preglacial and early glacial relics (33, 196, 201, 213).

Direction of migration and degree of relationship of populations of a species, such as may be determined by mass collection studies, sometimes lead to dating of isolation of a fragment of the population—as of the Indiana population of *Rubus odoratus*—where the relation to other populations is distant and leads to " the assumption that the isolation of *R. odoratus* in unglaciated southern Indiana greatly antedates the postglacial migration of that species into New York and New England " (75). Further consideration of such studies is better included in the next main section of this review.

Relic communities, isolated segments of vegetation unlike the surrounding vegetation and not successionally related to it, except as stages of one clisere may obliterate those of another, also occur. Most conspicuous of these are the boreal and prairie communities.

The boreal communities are readily interpreted as relics of the retreating migration of the more northern vegetation which once fringed a glacial margin. The age, however, may not always date from Wisconsin glaciation but may be earlier, as is evident from the preceding discussion of species ranges.

Prairie communities south of the glacial boundary are variously interpreted. They may be remnants of the eastward migration of prairie in post-Wisconsin time through what is now referred to as the Prairie Peninsula (200); they may be pre-Wisconsin or even earlier, perhaps augmented by post-Wisconsin migrations (27, 34). Several features contribute support to the latter hy-

pothesis: many of these prairie communities are more xeric than those on the Wisconsin drift in the area of the Prairie Peninsula; they contain a large number of species (about 150 have been listed), most of which are common to the western prairie and prairies of the Prairie Peninsula, and in addition, species absent from the Prairie Peninsula which occupy xeric habitats southward (as *Agave virginica*), and species which have evidently come from the south and southwest (see section on Prairie Relics). The southern xerophytes, the decided disjunction of southwestern or Ozarkian xerophytes, the distribution of such species as *Asclepias viridis,* whose range is said to be of great age (217), and as *Leavenworthia uniflora* (16) which do not extend across the glacial boundary, and the varietal differences in *Silphium terebinthinaceum* and perhaps in other species, as well as community relations, suggest that the separation of these prairie communities from the great western prairie may not have been contemporaneous with the post-Wisconsin eastern expansion of prairie, but may have been consummated at an earlier date (34). Such features indicate a spread of xeric elements, not from the prairies of the Upper Mississippi Valley but from the Ozark region and southward. These prairies are the communities referred to by Deevey (66) as "patches of a xerophytic (*Andropogon scoparius–Bouteloua*) type of prairie community, containing no western elements, but instead coastal-plain elements such as *Agave virginica* and *Ophioglossum Engelmanni*" which misrepresents the statements made in the literature cited. Neither were these "patches" said to be "northwestern outliers". Frequent use of the word "patch" implies small size, whereas some of these prairies were hundreds of acres in extent.

The question arises—can all of the floristic features of the glacial border be explained as post-Wisconsin and due to existing or recently operating environmental factors? It appears that workers familiar with the field aspects of the problem believe that they cannot; that the "occurrence and local distribution of the biota cannot be understood simply by analysis of climatic, edaphic, and biotic factors of the environment on either side of the boundary at a point in time, but that they must be interpreted also in the light of the history and inheritance of the organisms themselves in relation to this history of the soils and land surfaces" (155).

What reasons, based on vegetation alone or existing conditions,

are there for believing in the possibility of persistence? We might turn to the "nunatak hypothesis" in its modified form. At high latitudes today plants grow at the borders of the Greenland ice-cap (1), and on spots completely surrounded by glaciers—on nunataks in the Greenland ice-cap where scattered plants are found (1), and at altitudes of 4100 to 6000 feet in the Fairweather Range of Alaska where little patches of flowers and "turf-banked terraces" occur (56). At much lower latitudes (38°–40° N) temperatures must have been much less extreme, even at the maximum of continental glaciers, than at the margin of the Greenland glacier today, length of warm season longer, angle and intensity of sun greater. Consequently it may be expected that a greater variety of species could have survived. It appears "not impossible that we now have in the region of the glacial border species whose ranges of tolerance are or were sufficient to allow them to survive the periglacial climate with its attendant instability of soil" (155).

The great range in temperature in microclimates of different habitats of a limited area enters into the problem of persistence. A difference of 39° F. in minimum temperatures has been recorded for unlike sites in one small area near the glacial border in Ohio (215). The distribution of such species as *Sullivantia sullivantii,* which at its southernmost station occurs near such northern relics as *Taxus canadensis* and *Acer spicatum,* suggests persistence since an early Pleistocene ice advance. So also does the distribution of *Dodecatheon meadii* var. *frenchii.* The distribution of *Styrax grandifolia,* of *Pachistima canbyi,* etc. also suggest persistence from early Pleistocene. On the other hand, some patterns of distribution are clearly related to Wisconsin and post-Wisconsin climates.

The floristic features of the glacial border are intimately associated with the question, "How far-reaching were the effects of glaciation?" to be considered later.

ENDEMICS OF LOCAL OR PECULIAR HABITATS

Local endemics and pronounced disjunction of range have always received the attention of phytogeographers, as has been apparent in several of the topics already considered. The absence of close relatives of some of our local endemics raises question as to their time and manner of origin. Concentration of endemics in

local and sometimes peculiar habitats, and association with these of pronounced disjuncts of various affinities, make it desirable to consider such concentrations of species apart from the topics above.

Although little has been written about Alabama endemics, that State, nevertheless, contains two interesting endemic species —*Neviusia alabamensis* and *Croton alabamensis*—which, although not in the same habitat, are in the same geographic area, the Warrior Coal Basin and Upper Cahaba Valley. The former is a member of a monotypic genus of the rosaceous tribe Kerrieae which contains, in addition, two closely related Asiatic monotypic genera, *Kerria* and *Rhodotypus*. It is hardy as far north as southern Ontario and Massachusetts. The latter belongs to a very large genus of chiefly tropical distribution and best represented in the Americas; it is an evergreen shrub of tropical aspect. *Sedum nevii* from two counties in Alabama—with *Croton* in one locality and with *Neviusia* in the other—differs in chromosome number from Virginia plants which are now called *S. glaucophyllum* (53). Two species, only slightly different morphologically, are represented in the complex, the Alabama one with a $2n$-number of 12, the Virginia one with a $2n$-number of 28 (13). The rare endemic, *Croomia pauciflora,* is here also, and, although it belongs to a genus with two Asiatic species, these are southern in distribution, and members of the family (Roxburghiaceae) range through tropical Asia and Malaysia to tropical Australia. A subspecies of the black cherry (*Prunus serotina* ssp. *hirsuta*), which possesses " the features which may reasonably be assumed to be ' primitive ' in *Prunus serotina*", is now localized in this area and in the hilly Gulf Coastal Plain area to be considered next (132). *Cotinus obovatus* (*C. americanus*), of extremely disjunct range and most abundant in western Texas, occurs farther north in Alabama.

The significance of such endemic and disjunct species was recognized over half a century ago by Mohr who wrote of these as " the slightly modified descendants of types belonging to an ancient flora, which have survived the changes our globe has undergone and have found a refuge in their present localities " (135). Obviously the relationships and distributions are such that distinct floras seem to be represented. The chromosome situation illustrated by *Sedum nevii* and its derivative supports the belief in a

refuge somewhere in the southern Appalachian Plateau of Alabama.

In one of his essays, Asa Gray immortalized one of the most striking and rare endemics of the Apalachicola river bluffs, a hilly area of the Gulf Coastal Plain—*Torreya* (*Tumion*) *taxifolia* (162). This genus is represented in Upper Cretaceous deposits of the Atlantic slope (21); "there are no records in the long interim, but somewhere through the 60 million years, representatives of the genus lived on, giving rise (on the American continent) to *Torreya taxifolia* of Florida and *T. californica* of California" (33). Li (123) lists four Asiatic species. Another even rarer endemic of this same area, *Taxus floridana,* belongs to a genus with a similar history, and with a similar but wider range, especially in north-temperate latitudes. This species of *Taxus* certainly should not be called a "northern disjunct" as suggested by Deevey (66); to do so seems to put emphasis on the genus rather than the species, which the same author states should be dealt with. It would appear that the ancestors of both species had persisted somewhere in the Southeast, perhaps over considerable area, but were finally restricted to areas which survived late peneplanation (Coosa) and Pleistocene submergence. A number of other endemics, as well as many inland species with disjunct ranges, occur here also. (See Upland–Coastal Plain affinities.)

Woodson (216, 217), using biometric studies in *Asclepias,* demonstrates the probable antiquity of a Floridian refuge which he calls "Orange Island". This he considers one of three major refuges—Appalachia, Ozarkia, and Orange Island—which "were available to the biota of the southeastern United States during the late Mesozoic and early Cenozoic", and upon which "the modern speciation of *Asclepias* is considered to have developed". Orange Island is the richest of the three refuges in endemic species and subspecies of *Asclepias.* The three subspecies of *A. tuberosa*—all of which are panmictic—could not have maintained separate existence in contact with one another, and are used to show that the three populations arose from a common ancestor independently and in isolation.

The lower Altamaha River in Georgia is known as the last refuge of *Franklinia alatamaha,* first discovered on October 1, 1765, and last seen in the wild state in 1790. Its habitat and history of

discovery, together with possible causes of extinction, have been discussed (103, 204), but its possible route and time of entry are in doubt. It is one of the more advanced members of the Tea Family, whose species are mainly tropical and subtropical; genera exhibiting the more primitive characters are represented in South America, the probable southern hemisphere land mass from which ancestral expansion took place (46). One of the widely separated localities for *Leitneria floridana* is the lower Altamaha River; this is the only representative of a family of doubtful relationship.

Outcrops of granitic rock in the Piedmont of southeastern United States, which are known as "Flat-Rocks" or "Cedar Rocks", "are without parallel in eastern North America and support a remarkable and more or less endemic flora" (131). These rock exposures vary in extent from spots but a few meters across to areas of hundreds of acres; some 6000 acres of rock are exposed in Georgia alone. Of about 200 species definitely identified with the flat-rocks, 44 are considered as the most "typical" or "characteristic", and more than one-third of these (17 species and varieties) are endemic on the flat-rocks, i.e., "they occur in nature on these exposures only"—a high degree of endemism or near-endemism for a small area. The occurrence of two species of monotypic genera, *Diamorpha cymosa* and *Amphianthus pusillus*, each with no near relatives in its family, and of a third, *Sedum pusillum*, sometimes separated as a monotypic genus, emphasizes the phytogeographic interest of the flat-rock flora.

"If the complete geographic ranges of the most typical members of the flat-rock association are mapped, it at once becomes evident that almost all the plants in question, if not confined to the flat-rock habitat, are Coastal Plain and Piedmont species which have affinities with species of the Mississippi Valley or of the Ozark Region or even of the western United States and Mexico". This points to the possibility of an element of the Piedmont flora being derived from semi-arid regions of the Southwest and of the Mexican highlands. The extreme antiquity of establishment of the group is indicated by the unique species and genera, and is dated as later than the Cretaceous seas which separated eastern and western North America and probably in Tertiary time or later. Its failure to invade the Blue Ridge is explained as due to the occupancy of that area by ancient mesophytic forest.

Based in part upon a study of weathering of the granite, of "weather pits" in the granite, and of failure of soil accumulation, the rocks are interpreted by McVaugh as being of great age, hundreds of thousands or perhaps millions of years. "The flat-rocks have not had any general covering of soil in recent geologic periods, and possibly have never had such a covering since the last general peneplanation of the Piedmont surface" (131). On the other hand, Oosting and Anderson (138) relate the origin of these exposures to factors which produced the Fall Line but believe that certainly there has been sufficient time for the development of a complete cover of vegetation. They also believe that "it is not unreasonable to suppose that at one time the rocks were completely covered with at least sufficient soil to support a meager forest" and that "with the advent of the white man, lumbering, fires, and erosion might well have exposed these areas where the rock was nearest the surface". They were noted by William Bartram in accounts of his travels in 1776 before any extensive activities of the white man in that area. Successional evidence indicative of possible closure of vegetation over the rocks is used in the one case (138); in the other, geologic evidence of rate of weathering, coupled with the peculiar geographic ranges of endemic species and the absence of any close relatives of three of these endemics (131). It would seem to be necessary that exposed rock surfaces had been continuously available within the general granite flat-rock area since the beginning of speciation of the endemics. It would also be possible, even probable, that at times some rocks became covered by a thin mantle of soil, only to be exposed again by windfall and/or erosion; that the slow succession which has been outlined (119, 138) occasionally culminated in the development of a shrub or even forest cover which could be easily destroyed by windfall or fire.

In the Cedar Glades of the Nashville Basin of Tennessee, where flat surfaces of Ordovician limestone are exposed, a number of endemic and near-endemic species occur. The vegetation of this interesting area has been described by several writers, and some of its species listed (105, 151, 152). Cytological investigation of the species of *Leavenworthia,* all four of which occur in the Cedar Glades of Tennessee, which is the center of variability for the genus, are enlightening. Only one species, *L. uniflora,* ex-

tends far beyond the confines of the Nashville Basin. *L. aurea* appears to be the oldest member of the genus "because of its southernmost occurrence, disjunct range, and lower chromosome number". It is suggested that the basic pattern of this complex "is a reflection of glacial influence and of topography of the Nashville Basin, which since mid-Pleistocene has been favorable for the establishment of many populations . . ." (16). The genus *Lesquerella,* with four species in this area, has its largest concentration of species in Texas and northeast Mexico, and is abundantly represented in intermountain areas of the West. It is suggested "that representatives of both genera migrated from the southwest into the Nashville Basin", there producing a number of distinct species (157).

The mid-Appalachian shale barrens of Virginia, West Virginia, Maryland and Pennsylvania have long attracted the attention of botanists because of the unusualness of their flora and particularly because of their endemic species (6, 11, 58, 59, 145, 185). The shale barrens occur particularly on slopes on the Brallier shale (a very resistant noncalcareous shale) and afford habitats more or less unique in the East. The endemic species and varieties of these shale barrens include some closely related to surrounding species of other habitats and not always recognized as distinct taxa, e.g., *Allium oxyphilum* and *Convolvulus purshianus;* some definitely distinct but whose relationships are evident although in certain cases remote; and one, *Pseudotaenidia montana,* which is the only representative of its genus. *Eriogonum alleni* and *Senecio antennariifolius,* with related species in the Rocky Mountains, are interpreted as derived from Rocky Mountain species or from an ancestral species which gave rise to the now separated eastern and western species (205, 206). *Trifolium virginicum,* related to the prairie species, *T. reflexum,* has a postulated origin in the Great Lakes area (206). *Oenothera argillicola* has some characters in common with western species, and in some respects is more like certain eastern species; its chromosome arrangement differs from both (183), and there are indications of different races on different barrens (145). The time of origin of the endemics has been variously interpreted: of *Eriogonum,* that its ancestors "crossed the continent and came down the Alleghenies during pre-glacial times, but subsequent climatic changes destroyed all trace of them,

leaving behind this single endemic species" (205); of *Senecio*, that the Tertiary ancestor of the Appalachian and Rocky Mountain species "grew somewhere in what is now central Canada" and that the descendants had migrated "far enough to escape the Quaternary ice sheets" (206); of the six species with relatives in the surrounding area, and probably the others as well, that "these plants evolved in their present habitat" and "since the last ice age" but perhaps from progenitors which had come in sooner (145). This last author bases his conclusions (*a*) on the fact that the endemics are well adapted in structure and physiology to shale barren conditions which he has determined by thorough field and laboratory investigation, and (*b*) on the belief that it "is unlikely that these barrens could support during the last ice advance the existing endemic flora, since the terminal moraine is less than 300 miles from the northernmost barrens". As all of the endemics and near-endemics are geophytes or hemi-cryptophytes, it is difficult to understand why one would believe that the winters during the cold phases of the Pleistocene should have been so severe at 300 or more miles from the ice as to eliminate such species if they were already there. Using a genetic approach, Stebbins (183) believes that "the plant association of these barrens appears rather to have been gradually built up over a long period of time through the addition at widely separated intervals of plants derived from very different sources". Not all the shale-barren endemics are confined to outcrops of Brallier shale; it is suggested that absence of competition in such open areas is a factor in determining the present distribution of the species (210).

CONTRIBUTING FIELDS OF BOTANY

Certain fields of botany whose contents are not ordinarily associated in our minds with plant geography yield data valuable in the interpretation of distribution patterns. Chief among these are evolutionary studies which give information on rate of evolution and speciation, evolutionary trends, and migration routes or shifting of floras; cytology and genetics, giving information, through chromosome and hybridization studies, of probable time of origin of taxa, of migrations and relationships; certain types of monographic studies; and biosystematy (48, 49), or the newer systematics with its study of "species as populations of living organ-

isms", and the tracing of clines and probable migrations with the aid of mass collecting methods or population sampling. The physiology of organisms, often expressed as tolerance range, must enter into interpretations of plant geography. Although few investigations have been made of length of day requirements of wild species (4, 137), there is more than a possibility of this being a controlling factor in some cases. Overlapping of various fields of botanical research is evident and their interdependence inescapable. The possible contributions of genetics and cytology to floristic plant geography were pointed out briefly by Raup (154), and the relations of several fields were discussed by Cain (38), to whom the reader should refer. A few citations from the more recent literature of these fields are illustrative; no attempt has been made to assemble a bibliography.

The great age of, and slow speciation in many of our common genera and genera to which some of our Southern Appalachian endemics belong are well known. Paleobotanic and distributional data are used in making estimates of comparative rates of evolution.

Evolution of angiosperms has been going on since some time prior to the Early Cretaceous, the time of "the first reliable record of their occurrence", which was in rocks of that age in Greenland. "Some of the fossils suggest an extended pre-Cretaceous history. Leaves of *Platanus* show no recognizable distinctions from those on living trees" (51). Stebbins (184) believes "we should expect to find periods of rapid evolution alternating with times of relative stability. . . . And this is precisely what has occurred". Four periods of rapid evolution are pointed out; the first of these was in Cretaceous time, the second "occurred throughout the world in the middle and latter part of the Tertiary", and "the third accompanied the advance and retreat of the successive Pleistocene glaciations". A fourth, just beginning, is the result of man's alteration of the earth's surface. Most of this evolution is on a relatively small scale. It was during the first of these that many of our modern genera became differentiated. In the second, speciation resulted in the establishment of modern forms and of the stock of closely related modern forms; the eastern American-eastern Asian relationship dates from this time. In tracing the developmental trends of leaves of *Quercus*, Chaney (51) states:

"The genus *Quercus* is represented by an abundance of leaves which show a trend toward increasing size and lobation to the middle of the Tertiary period. Judging from these foliar organs there has been little if any evolution among the oaks since the Miocene epoch . . .". Very many of our tree genera were more diversified in Miocene time than at present and more widespread (23).

The fossil record of the Pleistocene, at least as far as tree species are concerned, is largely but not entirely a record of existing species; some species have become extinct. This is particularly true in Europe (23). "The evolutionary changes during this epoch were less than those of the previous periods of rapid evolution for two reasons". The new climates were not greatly different from the climates of northern and alpine areas of pre-Pleistocene time, and the new habitats were poor in nutrients. Hybrids, and particularly polyploids, were favored, "so that evolution during the Pleistocene might be expected to involve chiefly allopolyploidy" (184).

The relation of cytogenetics to plant geography is illustrated by the statement: "One important generalization which undoubtedly holds good for the bulk of polyploid complexes . . . is that the polyploids are dominant in regions which have been only recently opened to occupation by plants, or which have been subjected to great climatic or other environmental changes, while the diploids tend to occupy the older, more stable habitats" (182).

The localization of diploids in old areas is illustrated by *Galax aphylla,* which has two chromosome races, a diploid and a tetraploid. Examination of the map showing distribution of chromosome races (12) reveals the interesting and perhaps significant fact that all plants examined from the Cumberland Mountains (including the southern extension to Lookout Mountain), the Allegheny Mountains, the western margin of the Cumberland Plateau and the Unaka Range along the Tennessee–North Carolina line were diploids; i.e., only the diploid race occurs in the area of maximum development of the Mixed Mesophytic forest climax, which is interpreted as the ancestral forest type of the Deciduous Forest (32, 33). In the Blue Ridge (in the limited sense, i.e., eastern range of the province by that name) and adjacent mountains and on the Piedmont, both races occur, while

only the tetraploid has moved out almost to the coast on the Coastal Plain in Virginia, i.e., onto a young land area. Other comparable examples follow: *Sedum ternatum,* whose diploid race "has been found in a relatively restricted area in southern West Virginia, southwestern Virginia, and eastern Kentucky" [i.e., in the ancient Cumberland Mountains and southern Allegheny Mountains (and contiguous mountains of the Appalachian ranges)] has a tetraploid race which radiates out from that area in all directions (14). *Sedum pulchellum* has a diploid race "in the western and southern parts of the specific area", in Missouri, Arkansas, Oklahoma and Alabama northward into Tennessee (i.e., in the area of ancient Ozarkia and the southern Appalachian Highland) and a tetraploid which has spread northward into extreme southern Illinois and the Bluegrass section of Kentucky (15). The situation in *Diospyros virginiana* is somewhat more complex: "a continuous distribution of the 60-chromosome race in the central and southeastern [older] parts of the specific area; a peripheral . . . of the 90-chromosome race . . ." (18). The basic number "appears to be 15". *Diospyros* is an ancient genus, 17 forms described from mid-Cretaceous rocks, known in the Eocene (?) of Panama, and now widely distributed in the tropics (23). This suggests that *D. virginiana,* the only species in our range and one whose tetraploid race has a range comparable to that of the diploids mentioned above, was long ago derived from a diploid ancestor of perhaps still more southern range. The aneuploid *Sedum nevii–Sedum glaucophyllum* complex and the *Leavenworthia* complex have been referred to in the section on endemics.

The very complicated situation in *Vaccinium,* where diploid, tetraploid and hexaploid species and many hybrids have been observed in the wild, has been investigated by Camp and his coworkers (43, 44, 45, 63, 64). The studies are for the most part a combination of cytogenetics and biosystematy. The genus is thought to be very old, and probably was highly differentiated in the Cretaceous. "The fundamental evolution apparently takes place on the diploid level and must be an exceedingly slow process" (43). "Morphologically, some of the basic, diploid blueberry species are so different that one is almost tempted to consider the group to have more than one line of descent; certainly, if they have diverged from a common ancestral stock, it must have

been fairly early in the Tertiary" (64). Several indications of age can be mentioned: the great diversification, which has resulted in segregation of subgenera (or genera according to some classifications); pronounced disjunction in some of these, for example, *V.* (*Hugeria*) *erythrocarpum* "has a homolog in China" (45), the vine-like *V.* (*Herpothamnus*) *crassifolium* of "restricted areas from southeastern Virginia to South Carolina . . . has much in common with a few South America species which are mostly epiphytic, pendant, lianae-like plants" or at higher elevations grow in soil (45). The longevity of individuals of some species of *Vaccinium* is remarkable, a factor which favors chance cross-pollination and persistence of individual plants "in advantageous microhabitats in the face of ecological changes"; one clone of *V. myrsinites* is calculated to be not less than 1000 years old; clones of the distantly related box huckleberry (*Gaylussacia brachycera*) may have "persisted for untold thousands of years, at least since the late Pliocene or early Pleistocene" (63). In contrast to the slow evolution at the diploid level, "speciation among polyploids may be relatively rapid, being, in part, a phenomenon of the current scene" (43). But some polyploids are old. Hybrids are numerous, and "it is likely that as many interspecific hybrid blueberries have been naturally produced in the last hundred years [after the advent of white settlers and the clearing of forests] as in the preceding ten thousand years. However, . . . certain natural populations (e.g., *V. corymbosum*), which today are widespread, are the result of mass hybridizations during and after the Pleistocene, the result of readjustments along the distributional margins of several homoploids, following large scale climatic and ecological disturbances" (63). The conclusions reached in the several papers on *Vaccinium* here cited are based upon extensive field and experimental-plot studies; they have led to interpretations of geographic distribution which are dynamic. These papers should be referred to in connection with statements made in the "Hypothesis of Pleistocene origin of existing distributions".

Introgressive hybridization, or "the gradual infiltration of the germ-plasm of one species into that of another as a consequence of hybridization and repeated backcrossing" (9), is apparent in many species populations and frequently gives evidence of past shifts in the ranges of species. This is particularly true of allo-

patric introgression, for it is introgression between species native to different areas. It can occur when and where species of these different floras come into contact because of climatic or geographic changes. Floras of the Southwest show frequent evidence of introgression because pluvial periods of the Pleistocene allowed mesic floras to expand and come into contact. On the other hand, species of the generally mesophytic East were not so affected, except toward the southwest. As a result of this, introgression along the Ozark-Texas axis is apparent in species so far analyzed which have a related taxon in that direction. Some introgression in eastern species comes from related taxa in the "Orange Island" Floridian area, in the Rocky Mountains (rarely effective in our area), in the North and occasionally from higher altitudes in the eastern mountains. Variability due to introgressions "is least perceptible in such floristically stabilized areas as the central interior plateaus of Kentucky and Tennessee" (9). Examples of variability due to introgression are: *Cercis canadensis,* introgression from the xeric *C. reniformis* of Texas and Oklahoma; *Phytolacca americana,* showing, in the Southeast only, introgression from the Caribbean *P. octandra; Juniperus virginiana,* unmodified in the central part of its range but showing introgression from the Southeast, the Southwest, the West and the North, with the northern race extending south on the Coastal Plain to about South Carolina; and sugar maple, also showing a mixture of species from several directions (9, 61, 70, 99, 100). All such research is based on study of variability in populations and analysis of the variable characters.

Monographic studies often yield significant data concerning relationships and probable antiquity of species or groups of species. The genus *Ranunculus,* well represented in most floral areas of North America except the prairie and plains grasslands, can be used as an example (20). "The Eastern Forest Flora is characterized by compact endemic groups of species with relationships to groups occurring in several directions. The high percentage of endemism indicates the antiquity of the probable separate invasions of the prototypes of these groups". Certain of the species and their varieties (*R. septentrionalis, R. hispidus, R. carolinianus, R. fascicularis*) "are connected with their Pacific Northwestern relatives . . . by a chain of mutual relatives occurring

across the southern part of the continent". Relationships indicate that the origin of this southern group of species may have been in Mexico or on the Pacific Coast, or possibly in the East, and that the migration was in Oligocene or Miocene time. *R. recurvatus* is related to and perhaps derived from a group now restricted to the Pacific Region. The wide-ranging *R. abortivus* may be the prototype of an aberrant group of a section of the genus (Epirotes) not otherwise represented in the East. Absence of members of this section "in the Northern Coniferous Forest is explained by the lack of aggressiveness of the section or its apparent inability to fill in the areas denuded by glaciers in the Pleistocene epoch".

It is becoming increasingly apparent that many problems in taxonomy and phytogeography can be approached by means of mass collecting and study of populations, their degree of variability and the direction of increase or decrease in the intensity of variable characters. The last may give evidence of direction of migration and sometimes of time of isolation or of migration (47, 70, 75-79, 161). Thus in a study of *Rubus odoratus,* the isolation of a southern Indiana population which differs from all other populations of the species studied, is assumed greatly to antedate the postglacial migrations into New York and New England which took place from the unglaciated area to the South and whose direction is indicated by progressive changes from West Virginia to Maine (75). A study of beech, based primarily on extensive population samples, has shown that three distinct basic types of beech are present, each with somewhat different ecological requirements. But in some places "the population is genetically highly complex". This condition is frequent in the area of late Pleistocene deposits, i.e., in the Beech-Maple Forest Region, and may account for the diverse ecological niches occupied by beech in this area (47). With the completion of this work we will know more about the probable time and course of migration of beech, and, by inference, of many other widespread but complex "species".

"A revision of the North America black cherries" (132) is of phytogeographic interest because it suggests time and place of origin of subspecies of *Prunus serotina.* Analysis of morphological characters points to certain features which are primitive

and which define the hypothetical ancestor of early Cenozoic or late Mesozoic time. A subspecies, *hirsuta,* with the ancestral characters is "now localized in two areas in the Southeastern United States—areas, it should be noted, which support numerous other relict endemics like *Neviusia alabamensis, Croton alabamensis, Croomia pauciflora,* and *Torreya taxifolia*". This is similar to a southwestern taxon, ssp. *virens* var. *rufula,* which also has primitive characters. Migration of the early forebears of *P. serotina* was from tropical or subtropical latitudes northward "on both sides of the North American continent, possibly during the Mesozoic". Distribution of *hirsuta* suggests its separation from the primitive stock at an early date. The widespread ssp. *serotina* is much more recent and "seems to have interchanged genes with the original populations wherever contacts were made". Therefore, if isolated populations of *hirsuta* had always been surrounded by *serotina,* they could hardly have maintained identity. The distribution of the complex is in the form of a V with apex in Central America. This distribution pattern is common to many phylads ("phyletic lines of closely related species") and suggests south to north migrations, sometimes with intervals of migration in the opposite direction (133).

VEGETATION PATTERN AND CORRELATION WITH PAST EVENTS

The present pattern of vegetation is the result of existing conditions of climate and local environment and of past conditions—extent and configuration of land, erosion cycles, climate and glaciation. Just as taxonomists recognize refuge areas and probable migrations, and point out the significance of endemism and disjunction, so must the ecologist delve into the past in an attempt to explain the present. From the great mass of material on the geology, paleontology and physiographic history of unglaciated eastern United States, certain facts and events may be selected which are necessary to an understanding of plant distribution and vegetational development.[5] Into this brief chronological account are woven references to the floristic relationships already discussed, thus coordinating the whole into a series of related events.

[5] These have been discussed by the writer much more fully in Part III of "Deciduous Forests of Eastern North America" (33) than can be done in this review.

A contrasting interpretation, which places great emphasis on the Pleistocene, will follow the more generally accepted history here outlined.

MESOZOIC HISTORY

The significant history begins with the Great Appalachian Revolution at the close of Paleozoic time. The Appalachian Highland then assumed something of its present area; the Interior Highlands (Ozark and Ouachita provinces) finally emerged from the sea. Beyond a doubt, these uplands were occupied by a land flora.

During the early Mesozoic era, reduction of the mountains and plateaus formed by the Appalachian Revolution began. A pre-Cretaceous peneplain—the Fall Zone peneplain—was produced, and after subsidence was covered by Cretaceous sediments. The so-called "Cretaceous peneplain" of many earlier writers is younger than Cretaceous. West of what is now the Interior Highlands, a vast epicontinental sea extending inland from the Gulf of Mexico effectively cut off this land area from the far western lands which extended southward into Mexico. An Ozarkian-trans-Pecos "peninsula" extended southwestward from the more eastern land mass. By the end of Cretaceous time this peninsula was connected with the land to the south in Mexico. For the most part the Cretaceous continent was low-lying and very different in outline from the present continent. The more or less V-shaped distribution patterns of many phylads, with the base of the V in Mexico or Central America, may have been initiated at this time (see Contributing Fields).

Botanically the late Mesozoic era is marked by the appearance of angiosperms in the fossil record of America, their rapid increase in numbers, and great expanse in area. From the beginning of the record in America some forms referable to living genera were found. The common ancestor of the four present-day subspecies of *Asclepias tuberosa* is believed to have existed in Cretaceous time (217). By the end of this era the modern aspect was apparent, and many genera of the deciduous forest—as *Quercus, Juglans, Fagus, Celtis, Sassafras, Liriodendron*—were represented in deposits of the Atlantic slope or Mississippi Embayment. Modern as well as ancient and now extinct genera of gymnosperms were also represented, as *Picea, Pinus, Thuja* and *Tor-*

reya (*Tumion*). The progenitors, then, of some of our common and widespread species, as well as of some of local and apparently relic distribution (as *Torreya* and *Pachystima*) were known in the flora of what is now southeastern United States. The climate was mild (spruce in these earlier deposits is not considered to be indicative of a cool climate), and without marked zonal differences; rainfall was abundant.

TERTIARY HISTORY

A significant feature in the physiographic history of the Cenozoic is the gradual emergence of the Atlantic Coastal Plain. Old areas (the Cretaceous continent of Paleozoic and earlier strata) and young areas (the emerging coastal plain) were separated by differences of the edaphic environment. To some extent such environmental differences must have influenced the development of a vegetation cover and the distribution of species during at least the earlier part of the ensuing Cenozoic time. Granite outcrops may have been exposed on the Piedmont, and if so, must have been populated by plants capable of adapting to the peculiar local environment (see granite flat-rocks in section on endemics). Uplift also initiated the Schooley cycle of erosion which culminated in Miocene time. Farther west, a water barrier of Paleocene time probably extended northwestward from the Mississippi Embayment to North Dakota and adjacent Alberta (the Cannonball Sea, marine sediments), temporarily cutting off Ozarkia from the East. In the Western Interior gradual draining of the epicontinental sea of Cretaceous time allowed vegetational expansion—well recorded in the fossil record of that area.

These events of Tertiary time were of great importance vegetationally. The erosional history is recorded in land forms still retaining something of their mid-Tertiary configuration and in other features related to that erosion cycle. The distribution pattern of major vegetation types, the relationship of species and subspecies, disjunction of ranges, and localization of endemics should be examined in the light of Tertiary history. The undissected expanses of the Cumberland Plateau, with their swampy depressions, are but slightly lowered remnants of the Schooley (or Cumberland) peneplain. Here are the disjunct occurrences of coastal plain species of ancient ancestry. The knobs and rounded hills (monad-

nocks) rising, sometimes a thousand feet above the peneplain level, are the abode of endemics and disjuncts. In the Southern Appalachians (southern Blue Ridge Province of physiographers), mountains several thousand feet in height remained—this area was not in Tertiary time reduced to peneplain status, and in this always unreduced area is the greatest concentration of endemic species with eastern Asian relatives. The western escarpment of the Appalachian Highland, and all other places where resistant rock outcropped, retained some topographic diversity. Here, too, are local endemics and disjuncts of ancient ancestry. The Coastal Plain gradually enlarged and became available to species migrating from the uplifting peneplain as well as to those entering from lower latitudes. The Mississippi embayment was reduced in size, but its alluvial sediments continued to present a barrier to free interchange of upland species at the same time that it afforded easy means of migration toward the interior.

While this erosional history was in progress, suitable sites for the preservation of plant remains occurred along the Atlantic and Gulf coasts and in the Mississippi embayment (the Paleocene Midway and Eocene Wilcox formations). Many genera with modern representatives in eastern United States were represented in the abundant Wilcox flora, as *Aralia, Asimina, Cercis, Liquidambar, Magnolia, Taxodium.* For the most part these are genera which by modern standards are thought of as having southern affinities or as best represented in lower latitudes. Representatives of many now tropical or subtropical genera were also present. The common genera of more northern latitudes—which were conspicuous in Upper Cretaceous floras—are lacking in Eocene deposits of southeastern United States, but continued on in the Western Interior and the Arctic, and, because of the higher elevations of the Southern Appalachians, probably remained in that area also. The fossil record is from lowland sites of deposition, and, as MacGinitie (125) has pointed out, it is difficult to determine the nature of upland forest; remains of upland plants are extremely scarce; species represented by the more abundant fossils probably grew near the site of deposition. Although much of the eastern American continent of mid-Tertiary time was lowlying, highlands were present and doubtless supported a flora differing from that of the lowlands.

The fossil record indicates a mild climate, perhaps warmer than that of Cretaceous time, and this, together with the growing connections with lands of lower latitudes, afforded opportunity for great shifts in floras and for infiltration of genera from southward. Also, Tertiary land connections in high latitudes, at the time of mild climates in the far north, account for the Asiatic and European relationships displayed by so many American plants, while reduction in extent of areas of great relief accounts in large part for the localization of Southern Appalachian endemics. Also, we find that the finest examples of Mixed Mesophytic forest climax—lineal descendant of the mixed Tertiary forest—are in areas where the Schooley peneplain was never perfected (the unreduced areas). The central position of this forest climax in the vegetation pattern is thus accounted for.

With uplift and warping of the Schooley surface, streams were given renewed cutting power, and a new cycle of erosion, the Harrisburg,[6] was initiated. Peneplains began to develop in many separate drainage basins, but never coalesced because of lack of time. Areas underlain by resistant rock were dissected but not greatly reduced. Continuation of, and even expansion in area occupied by mesophytes was possible. Distribution patterns of species and of forest types probably assumed something of their present form. The mountainous Southern Appalachians remained a haven for species restricted by the Schooley cycle of erosion.

The alternation of ridges and valleys which characterize the topography of the Ridge and Valley Province was then brought about. The infertile and thin soils derived from the resistant and often steeply dipping strata of ridges is, and doubtless was, favorable to the development of the Oak-Chestnut forest climax, as a derivative of the ancient mixed forest. Shale barrens must have been produced, and evolution of some of the species of the present barrens may well date from this time (see Appalachian shale barrens in section on endemics). The Piedmont was peneplained, only to be dissected again, thus exposing or enlarging granite outcrops. The Interior Low Plateau was formed but doubtless retained hilly areas where the mixed forest could survive. Erosion in the Interior Highlands reduced much of the land to peneplain

[6] For discussion of varying interpretations of peneplain age, see Braun, 1950, p. 494.

status, favoring the persistence of species of coastal plain swamps, but left two rugged areas (Boston and Ouachita mountains) where relic mesophytes could survive. The enlarging coastal plain of Late Tertiary time approached the present Coastal Plain in extent. Some hilly areas remained, as they doubtless had in the previous cycle, thus permitting continuance, in these sites, of species of the mid-Tertiary flora.

The fossil record of the late Tertiary—the time of the Harrisburg cycle of erosion—is very poor, both in the Southeast and in the Western Interior. The flora of the Gulf Coast resembles that now found there. In the Western Interior, increasing aridity (due to continued rise of land which first drained off the epicontinental seas and finally culminated in the uplift of the Rocky Mountains) is reflected in the nature of the fossil remains. Eastward retreat of the more mesic elements of the flora, or, toward the west, restriction to the more hilly areas, doubtless took place. The Oak-Hickory association was thus derived and came to dominate the Ozarkian area. The xeric western and southwestern element noted in the flora of the granite flat-rocks may have entered at this time. The map of distribution of *Asclepias* (*Asclepiodora*) *viridis* (217), which is considered to be a species "probably of great age", suggests this as a possible time of entry into southern Ohio and adjacent Kentucky.

The Harrisburg cycle was terminated by uplift in late Pliocene time. Ensuing erosion cycles have had no far-reaching effects, although they have produced a few local features affecting species ranges; for example, the Nashville Basin in Tennessee, with its "Cedar Glades"; the Coosa peneplain on the Gulf slope, and above which rise groups of low hills with their disjunct and endemic floras.

PLEISTOCENE HISTORY

A discussion of Pleistocene events may seem out of place in a review concerned with the phytogeography of unglaciated eastern United States. However, a knowledge of Pleistocene events and effects of glaciation is essential to the interpretation of the vegetation of the unglaciated area.

Glacial stages (times of ice advance) alternated with interglacial stages (times of ice retreat). During the former, great quantities of water were locked up in the glaciers; as a result,

sea-level was lowered and the shore line was seaward of the present coast; during the latter, sea-level was raised and the low-lying coastal plain was partly submerged. Sea-level is known to have varied as much as 400 feet, exposing more or less of the continental shelf when at lower levels, flooding the land when high. New land for plant occupancy and migration was exposed during each recession of the ocean.

The " glacial boundary " is a composite line, here following one, there another of the great ice sheets. At no time did glaciers cover the entire area within the " glacial boundary ". In a peripheral band the land surface was modified by outwash deposits, ponding of streams and drainage changes. Farther from the ice front, topography was unmodified except by normal erosional processes, or locally by deposition from overloaded streams fed by melting glaciers.

The last or Wisconsin glacial stage is divided into four substages, between which there were partial withdrawals of the ice. The ice of the last of these substages (Mankato) did not reach as far south as earlier advances.

The fossil record of life in Pleistocene time is meager. A few plant fragments (leaves, fruits, seeds, wood, and rarely stumps in situ), mosses and pollen occur in organic deposits of interglacial stages and tell something of the vegetation north of the glacial boundary in these interglacial times. Carbonaceous lenses in Pleistocene terrace deposits of the Atlantic and Gulf coasts and Mississippi embayment contain some plant remains, but exact age of most of these deposits is doubtful. Pleistocene deposits along Little Bayou Sara in Louisiana, where stumps of *Taxodium distichum* and *Nyssa sylvatica* (or *aquatica*?) occur, are of particular interest because of the admixture of northern and southern species—*Larix laricina* (wood), *Picea glauca* (wood, twigs, needles, cones), *Thuja occidentalis* (small fragments of branches), together with such southern species as *Taxodium distichum, Chamaecyparis thyoides* (small piece of wood), *Diospyros virginiana, Quercus* spp., and many widespread species (red cedar, walnut, hickories, beech, tuliptree, boxelder, cucumber-tree). This has been explained by stating that the northern element dovetailed into or telescoped into the warm-climate vegetation, and that each occupied suitable sites (35).

All macro-fossil deposits indicate persistence of an occupying

vegetation comparable to that of today, and an infiltration of more northern species. Pollen records tell another story which must be correlated with dating of deposits.

DATING OF DEPOSITS. Many million years have elapsed since the beginning of angiospermous vegetation in America, and about one million years have passed since the first continental glacier started its advance.

In a chapter on "Pleistocene Chronology", Flint (87) has reviewed the various methods used in attempts to ascertain the length of time since glacial retreat from certain areas. Among these are rate of recession of falls, rate of sedimentation on deltas and on lake floors, rate of accumulation of peat, rate of precipitation of travertine—in all of which a number of variables are involved. Varves have been used with considerable accuracy in limited areas, although errors may arise in making correlations from place to place (10).

Attempts to estimate the lengths of glacial and interglacial stages of the Pleistocene are generally "based on comparison of the progress reached by some process, such as weathering or general erosion, during some stratigraphically known time, with the progress reached by the same process in postglacial time within the same region" (87). Depth of leaching of soils and amount of material lost by erosion have been used in several places. Such calculations are based on an assumed 25,000 ± years for the amount of time since the last (Mankato) Wisconsin ice maximum.

Measurement of radioactivity of residual Carbon 14 in organic remains is the latest method being used in the measurement of postglacial time. Measurements made at the Institute for Nuclear Studies, University of Chicago, and at the Lamont Geological Observatory of Columbia University appear at intervals in Science. Some of these measurements, such as those made from wood or peat in glacial deposits, are of particular interest for the phytogeographer (see Radiocarbon Dates (153) in Bibliography). For example, the age of a sample of peat from Singletary Lake, N. C., is given as "older than 20,000"; cypress wood buried under sand deposited by the Santee River in South Carolina is "older than 17,000", and cypress wood from Myrtle Beach is "older than 20,000", which would appear to date back at least as far as Cary time. On the other hand, the age of peat from Cranberry Glades,

W. Va., is 9423 ± 840 years; from Cedar Bog Lake, Anoka County, Minn., 7988 ± 420 years; of wood and peat from the Two Creeks forest bed in Manitowoc County, Wis. (by far the most interesting late-glacial deposit known; see section, "How far-reaching were effects of glaciation?") is approximately 11,000 years (figures range from 10,877 to 12,168). All of these are of the same order of magnitude, and all are Mankato or post-Mankato (153). All are notably less than estimates arrived at by previous methods.

Under the title of "Radiocarbon dating of late-Pleistocene events", Flint and Deevey (88) have brought together much of the significant material of the short period of radiocarbon investigations. For the purposes of this review, their most significant statements are: "The time of attainment of the Boreal type of climate, i.e. the time of the pine zone, differed appreciably according to the latitude of the locality. The pine zone is about 9,000 years old in West Virginia, about 8,000 years old in Connecticut, and about 6,000 years old in Maine; it is about 8,000 years old in southern Minnesota and about 7,000 years old in northern Minnesota. The age of the thermal maximum (climatic optimum) has not been precisely fixed, but several samples from horizons not far from it give ages ranging from about 6,000 to about 3,000 years ago".

The radiocarbon measurements give more definite dates than have hitherto been possible; they demonstrate a shorter time interval since the Mankato maximum than has previously been postulated. Thus the reconstruction of events in late-glacial and postglacial time should be correlated with these recently ascertained dates. A limitation of the method has been that it could not be applied satisfactorily to material older than about 12,000 years; however, recent advance in technique (153) "permits dating back to 30,000 years".

THE POLLEN RECORD. The pollen record of late-glacial and postglacial time is one of the chief sources of information concerning migration and the development of vegetation within the glaciated area. South of the glacial boundary, pollen records are few and often incomplete. Most of them contain some spruce or fir at the lower levels, indicating some infiltration of northern genera; most,

but not all, show considerable agreement with existing surrounding vegetation. When spruce is present, this fact is always emphasized, but the presence, at the same level, of pollen of trees of more southerly range is seldom mentioned, although it may be as reliable a climatic indicator as is spruce.

No attempt is made here to review the literature on pollen profiles, for that is beyond the scope of the present review. Only those of particular phytogeographic interest will be considered. Most significant are the pollen profiles from a Texas bog, from bogs in the New Jersey Pine Barrens and from the Carolina bays (depressions in the Atlantic Coastal Plain).

The features of greatest significance in the 22-foot Texas pollen profile are "the presence of pollens of *Abies, Picea glauca, P. mariana* and *Castanea*". The first three of these are essentially confined to the lowest levels, and total only silghtly more than two per cent of the 1450 pollen grains in eight of the foot-levels. The last (*Castanea*) occurs almost throughout the record; it is present with spruce and fir at some of the lower levels, and reaches a maximum about two-thirds of the way toward the top. The limit of its present range is 100 miles to the eastward. "Climatic changes suggested by the vegetation are: cool (boreal conifers), to warm-dry (*Quercus* and grasses), to warm-moist (*Alnus* and *Castanea*), to warm-dry (*Quercus, Carya,* grasses), becoming still drier towards the topmost level in the bog" (150).

Pollen profiles from bogs in the New Jersey Pine Barrens not far south of the glacial boundary show a "total lack of a successional trend in the forest history". They suggest "a highly mixed forest cover in which northern conifers were associated in a minor way with southern broad-leaved genera" and seem to justify the conclusion "that unglaciated New Jersey was during Wisconsin times a refugium for southern broad-leaved trees, with intrusions of the association by such boreal genera as spruce and fir" (146, 148).

Recent studies in North and South Carolina afford the most complete information yet available (90–92). These have the advantage of radiocarbon dating of certain horizons. In the pollen diagrams of eight cores taken from "bays" in the southeastern portion of the North Carolina Coastal Plain, pronounced vegetational changes are recorded. The record is said to begin with

early Wisconsin, probably Iowan, time and extend to the present. *Picea* is present in small amounts at all levels older than about 10,000 years (radiocarbon dating), and it is of interest to note that *Liquidambar* and *Taxodium* were often present at the same levels as *Picea* and in comparable amounts. A pine-spruce maximum at a depth slightly greater than that of the dated horizon is believed to be of Mankato age. Size of the pine pollen indicates that it was not one of the species now on the Atlantic Coastal Plain. Increases in the pollens of broad-leaved mesophytes are believed to be contemporaneous with interglacial subages. Frey believes that if the forest of the Southern Appalachians " was perhaps displaced only to somewhat lower elevations, then one might expect that a substantial occurrence of hemlock, elm, hophornbeam, and perhaps beech, at the present locations [Carolina bays], would be correlated with a glacial advance, or in other words with a maximum depression of climate. This is contrary to the present findings ". It appears from the diagrams that occurrence of the above-mentioned mesophytes is contemporaneous with occurrence of sweet gum and bald cypress, and large amounts of oak and hickory, a combination not unlike that occurring on parts of the Coastal Plain at the present time. No adequate explanation is offered for the pine-*Isoetes* maxima of the Cary and Mankato subages, when mesophytic trees and higher aquatics are almost absent except in the overlap to adjacent horizons, and bog shrubs and sphagnum greatly reduced. Such a flora might indicate lowering of the water table so that the lake level was reduced to a silt flat covered with shallow water and hence favorable for a prolific growth of *Isoetes* with perhaps a border of bog shrubs, and the surrounding forest was too dry for most broad-leaved trees. As an objection to such a xeric hypothesis, Frey notes the presence of peridinians, a part of the microfauna. An alternative explanation involving local deep burning of the peat and redistribution of peat through erosion has recently been advanced (203). Any fire which burned out the peat of the bog would doubtless have extended through surrounding forests; dominance of pine can be brought about by fire. " Climatic fluctuations undoubtedly occurred, correlated with advances and retreats of the Wisconsin ice sheets. Purely by inference at this time it is believed that the climate at more inland locations also varied during this period and

that the climax forests of these locations probably experienced considerable displacements" (92).

The North Carolina pollen profiles present a number of problems which have not yet been solved. They show that there were pronounced fluctuations in vegetation near the coast, but they can give no indication of how far inland such changes occurred. They suggest that at no time during the Wisconsin age did Appalachian forests move near enough to the coast to affect the pollen record; if they had, surely the dominant chestnut, with abundant windborne pollen, would have been recorded. Considering the edaphic requirements of most of the species of the cove hardwoods, they could scarcely be expected near the coast.

The evidence derived from pollen profiles must be considered in connection with all other sorts of evidence bearing on the phytogeography of eastern United States.

AN HYPOTHESIS OF PLEISTOCENE ORIGIN OF EXISTING DISTRIBUTIONS

An unusual viewpoint, one very different from that held by the majority of plant geographers, and which brings the influence of the Pleistocene into great prominence, has been expressed by Edward S. Deevey, Jr. (66). It is based upon the fact that the Pleistocene has intervened since the species arose "in the Pliocene, or earlier", and upon the belief that "there has been sufficient time, and sufficient transfiguration of geography, for the pre-Pleistocene distribution pattern to be completely transformed in a very large number of cases". This is the thesis of a lengthy paper on the "Biogeography of the Pleistocene", in which its author states that "documentation follows at some length". This "documentation" is largely a matter of reinterpreting the works of many authors, sometimes with the original material so distorted that it is scarcely recognizable. A great deal of the literature used is zoological, but only the botanical topics are included here.

Deevey believes, as do many biogeographers, "that existing ranges of species and of larger groups are the product not of existing geographic conditions but of all geographic conditions obtaining throughout the history of the species or stock", but that it certainly should not be assumed "the existing distribution pattern of the species to be as old as the species itself, or as the genus or

family to which it belongs". He feels that "most or all of [certain curious disjunctions of distribution] are explicable in the light of postglacial climatic changes".

As a working basis, several "principles" are set forth. One of these is, "We deal with species, not with families or orders". Another, called the "Economy of hypothesis", is of particular interest to all concerned with plant geography, for it states: "No distribution is taken to be old unless it can be proved not to be young .... All distributions of species are taken to be of Pleistocene date in the absence of good proof that they are older". One may well ask, what constitutes proof? Deevey further states, in connection with "Origin of species", that "nearly all well-studied cases of subspeciation and speciation point to the Pleistocene as the time of such previous isolation, and the occurrence of related forms in the same area is therefore attributed to post-Pleistocene alterations in geography and in biogeography".

The present knowledge of glacial and postglacial stratigraphy and fossil floras of North America is said to be inadequate; the stratigraphic detail of most deposits has not been worked. Whether such interglacial floras as those described by Steere (187) and by Rosendahl (158) represent all or part (and what part) of an interglacial subage, is not known. On the other hand, great strides are being made in postglacial stratigraphy, with the help of pollen analyses.

A brief résumé of postglacial pollen chronology with comments on the Xerothermic Interval and glacial refuges offers suggestions which need serious consideration in connection with other interpretations. Pertinent are the discussions of evidence of a tundra belt, of the migration of certain tree species, of the somewhat more northern range limits of certain trees in the Xerothermic Interval, and of conditions south of the glacial boundary.

The existence of a tundra belt has been reported in Aroostook County, Maine, on the evidence of a large amount of grass and sedge pollen at lower levels of the bog profiles (68). However, it has been pointed out (149) that pollens of sedges, alder and ericads, together with spores of mosses and ferns, characterize tundra, not pollen of grasses. Lack of evidence of a tundra belt is explained (66) as probably resulting from the fact that the basins, which later became occupied by bogs, were filled with

stagnant ice long after the main body of the glacier had retreated and until a less northern type of vegetation had surrounded the basin. It is claimed that the belief of most plant geographers that the tundra belt in the Middle West was very narrow is based mostly on negative evidence. However, evidence based on fish distribution is said to suggest that " a subarctic tundra zone must have followed the retreating ice front across the northern United States and Canada . . . but the tundra must have been very narrow and impermanent, and the modern flora and fauna immigrated astonishingly early ".

" Pollen analysis has not been very helpful in establishing the location of refuges. In fact, as evidence accumulates that boreal forests were widely developed in the southern United States at about the climax of the last glaciation, it is becoming increasingly difficult to imagine a place where the characteristic components of the temperate flora could have taken refuge ". Nevertheless we find statements about " beech, moving out from its center of refuge in the northern Appalachians " during an early warm interval of postglacial time, and " hickory, moving eastward from centers of refuge in the middle West " during the ensuing warm dry interval, the Xerothermic Interval. The pollen sequence reflects phytogeographic movements. The evidence for " widely developed boreal forests " is based upon pollen and macro-fossil deposits already discussed (see Pollen Record), all of which are in a peripheral position as far as deciduous forest is concerned, and in locations (except the Texas bog, in which *Castanea* was contemporaneous with *Picea*) where it is possible or even probable that adjacent bodies of water, cooler than today, tended to lower summer temperatures. Deevey places great weight on the pollen of the Texas bog and on the plant remains in Little Bayou Sara deposits in Louisiana because " members of the northern Coniferous forest community occurred during the Pleistocene " as far south as Texas and Louisiana, which he believes means that, " unless one can believe that the typical temperate species were pushed south of the Rio Grande and deep into peninsular Florida, the alternative is a picture of an extraordinary intermingling of boreal, temperate, and subtropical elements along the Gulf coast (and on land now submerged along that coast by a postglacial rise of sea level) ". In neither case does the fossil record show any sub-

tropical species to have been present—the assemblage is one of deciduous forest species with an admixture of coniferous forest species; those of most southerly distribution (*Taxodium* and *Nyssa aquatica*) now range northward to southern Indiana and southern Illinois but are most abundant in the South; the magnolia is *M. acuminata,* which now ranges from Oklahoma, Louisiana and Georgia northward to the high Allegheny Plateau of northwestern Pennsylvania and western New York. Comparable assemblages are not uncommon today; for example, bogs in southern and western Connecticut where the southern white cedar (*Chamaecyparis thyoides*) and the northern black spruce (*Picea mariana*) sometimes occur together (136); the Carter Caves and Tygarts Creek forest in northeastern Kentucky where northern disjuncts (as *Taxus canadensis* and *Acer spicatum*) and Appalachian species of southern range (as *Magnolia tripetala*) occur together (33, pp. 111, 479).

The topic "Southeastern United States during the Pleistocene" is replete with material that needs critical examination. The area seems to include all of eastern United States south of the glaciated area, and is much more extensive than usually included in the Southeast.

The eastern American–eastern Asian relationship already discussed is pointed out, and animal and plant examples are mentioned. "There are various reasons for believing that the biogeographic connection implied by such disjunctions is old. Chief among these are the numerous instances where paleontologic evidence is available, showing that the present ranges are fragments of a formerly more continuous distribution". The few cases of specific identity among plants (none is known among animals) are attributed to low rates of evolution. This would account also for the slight varietal differences displayed by many plants of eastern American–eastern Asian range. "In general, then, the biota of the southeastern United States is dominated by a large number of relicts of the Arcto-Tertiary forests, which had their floristic origin in the Cretaceous, were holarctic during the early Cenozoic, and gradually withdrew into the tropics in response to slow and interrupted cooling of the northern continent". Dominated by relicts that withdrew into the tropics—and came back again? Many Eocene genera of the Wilcox flora did withdraw to the tropics and now

compose a considerable fraction of that flora, and many seem to have remained in temperate latitudes. Because latitudinal shifts of floras are demonstrable for early Cenozoic time, certain implications are believed to be involved: "Pleistocene climatic changes were more drastic than those of the earlier Cenozoic and accelerated the extinction of some stocks and the permanent withdrawal of others into the tropics. In addition, the present picture of Cenozoic climate and life suggests that the whole assemblage of species now living on the northern continents (and in the northern oceans) is of Pleistocene origin. It is difficult to see how cold-climate . . . plants can have arisen except under a climatic regime at least as glacial as today's". But we know, from instances of specific identity or slight varietal differences of American and Asian species, that many of our species antedate the Pleistocene by several epochs. If it were not that these statements come under the heading, "Southeastern United States", one might suppose that arctic and subarctic species were referred to, but this is not the case. The southern Appalachian and coastal plain floras are included in the material that follows. As the Southern Appalachians have long been "supposed" to harbor old relicts, Deevey feels that the question of "suitability of the Appalachians as refuges for ancient species during glacial stages of the Pleistocene" must be reopened. This is done by taking up and reinterpreting the works of others, and in some cases changing some of their basic statements.

The complicated problems connected with hybridization in *Vaccinium* (43) are brought into the picture. Referring to the three species (*V. arkansanum, V. simulatum, V. australe*), which gave rise to *V. corymbosum,* the statement is made that "Camp supposes that in pre-Pleistocene time these three species had parallel but not contiguous ranges essentially as today". Camp states that "there is evidence that they arose from different sets of diploids probably no later than the mid-Tertiary during an early period of active speciation resulting from the geographical rearrangement of diploids", and goes on to explain what he believes, as a result of long-continued research, brought about the final synthesis of *V. corymbosum.* But Deevey believes that "this is no doubt an unnecessarily complicated hypothesis; presumably one glacial age would accomplish what seems to Camp to require

several" and that "the fragmentation of ranges that led to the production of the older species, assuming it also to be of Pleistocene age, implies a considerable history of Pleistocene geographic changes *deep in the nonglaciated territory*". Camp believes there is evidence for the mid-Tertiary date; Deevey assumes the Pleistocene date.

The well-known *Iris* problem (7) is cited, a problem involving the discovery of parents of *Iris versicolor,* i.e., *I. virginica* var. *shrevei,* "ranging from the coastal plain through the northern Appalachians and overlapping the range of *versicolor*" (66); and the previously unrecognized *I. setosa* var. *interior* in unglaciated central Alaska. Anderson gives for the range of *I. virginica* var. *shrevei,* "Mississippi Valley and Great Lakes region from southern Minnesota and southern Ontario, southwards to Texas and Alabama"; his map shows few Appalachian stations and no coastal plain stations. According to Deevey, Anderson states "that *versicolor* was synthesized when Pleistocene glaciation mingled the populations of *setosa* var. *interior* and *virginica* var. *Shrevei,* presumably along the margin of the Wisconsin ice sheet in Minnesota and North Dakota". But Anderson states that "*Iris versicolor* is either late pre-glacial or inter-glacial" and that "the present distributions of the species would suggest that the original hybridization (or hybridizations) took place in the interior of the continent, perhaps in the general region of the present-day Great Lakes". Further, he thinks that "very anciently the *Iris virginicae* of the Atlantic seaboard became slightly differentiated from those of the Mississippi Valley", thus carrying the evolutionary pattern well back into Tertiary time. Anderson's statements are based upon "a detailed morphological census" extending from Alabama and Mississippi to northern Michigan.

In discussing the problem of endemism, the necessity of determining the kind of endemics is pointed out. A localization of endemics, even if from several genera, does not necessarily indicate great age. If such endemics are surrounded by related widespread species, they are young. (See certain endemics of the shale barrens.)

More evidently within the province of plant geography is the discussion of "persistence of plant communities on the Schooley peneplane". In the first place the relative values of disjunct oc-

currence of a single species and of disjunct occurrence of a community are discussed. Most plant geographers consider the latter to be more significant (55, 94), but no plant geographer has ever stated or implied that there is any "geometrical progression" involved, or that the occurrence together of ten species of the same community is "n^{10} times as remarkable as the occurrence of one of them". However, Deevey, in a later paper dealing with marine hydroids (67), says that "one such example of disjunct range might be the result of an accident, either of dispersal or of collecting, and the repetition of the phenomenon merely increases the likelihood that the problem is real". The question at issue is the occurrence of coastal plain colonies in swamps on the Cumberland Plateau where the old-age topography of the Schooley peneplain still persists, i.e., on undissected remnants of that plain (29, 30). In support of the idea of separate and presumably recent invasion of these swamps by coastal plain species, Deevey outlines briefly the classic principles of "invasion of new habitats" and subsequent succession—the sort of invasion and succession which marks every depression on the young glaciated area. But on the old-age surface of the Schooley peneplain, invasion was not into new habitats. Neither is this a "place where plants of open, dry country, including some grassland species, come largely into question". A few species do occupy sites comparable to the Pine Barrens; most are in boggy swamps, carpeted with *Sphagnum* and *Pallavicinia*, and none, except the ubiquitous *Andropogon scoparius*, a complex species of many races with distinct range, could possibly be called "grassland species". This misinterpretation of floristic content of the communities may be at the root of a suggestion, made later in the paper, that "it may have been during the xerothermic interval that the plants moved into the interior". The complete absence of western species makes this very unlikely. A further misinterpretation of floristic content may in part be responsible for the attempt to line up these relic coastal plain swamps with northern bogs, for the statement is made that the "colony of ten coastal-plain disjuncts on an undissected portion of the Cumberland Plateau is accompanied by northern species, elsewhere rare in the region". The few somewhat northern species that are present are common and have wide ranges. Unfamiliarity with the terrain is probably responsible in part for the

statement about " the inherent unlikelihood . . . that plants remain on a patch of ground while the ground is uplifted by hundreds of feet and deep valleys are cut all around ". The " ground " which was uplifted was the entire Schooley peneplain. As was frequently emphasized, the vegetation of the once low-lying plain became gradually restricted as the area of the plain became smaller; hundreds of square miles still remain, and " deep valleys " are miles away from the larger flats which still harbor coastal plain species.

The comments concerning brief statements on the location of areas of best development and of disjunct occurrences of mixed mesophytic forest climax (32) seem much confused. For example, the statement is made " (1) that many of the important species and the mixed deciduous forest itself stop at the glacial boundary ". Against this must be balanced the original statement that " the two most characteristic species of the Mixed Mesophytic forest, *Tilia heterophylla* and *Aesculus octandra,* are abundant to the glacial boundary and into the area of Illinoian glaciation, but have scarcely invaded the area covered by Wisconsin ice ". Another statement, " (2) that ' the mixed deciduous forest . . . is as rich in species in all layers near (not at) the glacial boundary as it is 200 miles farther south ' " is, in the original, not what is presumably quoted, but " the rugged western margin of the Appalachian Plateau harbors excellent mixed mesophytic forest which is as rich . . .". Mixed mesophytic and mixed deciduous are far from synonymous, which at once makes the misquotes untrue. And the stated location, " rugged western border ", introduced factors not present elsewhere. The fact that the change is near, not at, the glacial border refutes the value of arguments about differences in ecologic factors on the two sides of the boundary; those differences are apparent but are not the causes of the change in forest communities.

Throughout the discussion concerning the idea of persistence (*a*) of coastal plain plants on remnants of a former peneplain, and (*b*) of certain species generally thought of as Tertiary relics of Asiatic relationship in the always unreduced areas, there seems to be confusion about the terms " reduced " (which means reduced to peneplain) and " unreduced " (which means not reduced to peneplain, but always hilly or mountainous). For note: " the

species believed to have existed on the low-lying Miocene erosion surface [these would be the coastal plain species] . . . ought either to be confined to residuals of that surface [they are] or to have spread out subsequently [some have]; they ought not to *avoid* peneplane remnants [within the whole Appalachian Highland, they do not]. But this is just what some of them do; against *Stuartia malachodendron* [which is on the Coastal Plain and nowhere mentioned in the literature cited] and *S. pentagyna,* American species of an otherwise Japanese genus, confined to Schooley remnants [*S. pentagyna* is confined to always unreduced areas, and is not on Schooley remnants], we may balance *Shortia galacifolia,* confined to a low area at the inner edge of the Piedmont [its occurrence in several places in the always mountainous Blue Ridge province has been discussed under "Extra-Continental Relations"] ". That is, *Stewartia pentagyna* and *Shortia galacifolia,* and many other of these ancient species are in the areas never reduced to peneplain.

A final topic under "Southeastern United States during the Pleistocene" is one dealing with the effectiveness of glacial climates south of the drift border. This is best considered in connection with the next section of this review.

Other topics concerning glaciated eastern North America, such as northern relicts and survivals from interglacial ages, have already been included.

It is of interest to see stated in the "Summary", one of the reasons for promulgating the hypothesis of Pleistocene origin of present distributions: "Because the attempt has never been made before, and therefore seemed eminently worth making, there has been an effort in this presentation to look at existing animal and plant distribution as a whole from the standpoint of Pleistocene geography". As a result of this viewpoint, these summary statements concerning the "Southeast" are in order: "If the species have been in their present habitats . . . since early or middle Cenozoic time, it is difficult to understand the obvious fact that Pleistocene climatic changes in the general region were extensive. [See next section for discussion.] That is, the evidence from Pleistocene fossils [in coastal areas] conflicts with the pattern of existing distribution as interpreted by biogeographers". Therefore, "the relicts on peneplane remnants must have been moving

around during glacial ages, some of them perhaps having been driven into Mexico and peninsular Florida".

This contribution to biogeographic thought will challenge opponents and proponents of the theory to more careful and precise statements of facts on which their beliefs are built. Further evaluation of the hypothesis is best included with the discussion to follow.

HOW FAR-REACHING WERE THE EFFECTS OF GLACIATION?

In order to evaluate the interpretations made in regard to general distribution patterns and to the many specific cases which have been reviewed, it is necessary to consider the very important question—How far-reaching were the effects of glaciation? The direct physical effects—deposition of till and outwash, ponding of streams, drainage changes, etc.—are well known. The effect on climate can only be inferred from evidence at hand, and climate is of great importance in the geography of plants. Some of the inferences are based on physical features of the land and water, some on Pleistocene fossils, some on cytogenetics, chromosome numbers and introgression, and others on distribution patterns of present-day vegetation.

Bryan (36) believes that an arctic climate must have bordered the ice at each advance; however, he suggests that the zone of periglacial climate may have been very narrow in some places because the plains area in the interior United States allowed a free sweep of southwesterly winds. The distance beyond the ice sheet to which the glacial anticyclonic winds would be effective would thus be modified. Where such cold winds were overlain by moisture-bearing winds from a southerly direction, clouds, rain and fog would be produced. Such effects could be expected if, as Berry (23) believed, it is "probable that the extensive Pleistocene glaciation was due more to unbalanced precipitation than to any great degree of secular change in temperature".

Raup (155) suggests that boreal land-form studies may be useful in connection with problems of the glacial border. As the effects of frost action are a function of climate, we should look for "the effects of this climate and its attendant frost action in the soils and topography" both beyond and within the glacial border.

As yet, the study of frost phenomena is in comparative infancy. Recognition of ancient frost forms is often difficult. Various solifluction features, block fields, rock streams, fossil or ancient stone rings and stone stripes have been recognized in temperate latitudes, both within and without the glacial boundary (69, 155, 178–180). Evidence of congeliturbation (of debris produced by frost-riving and moved by solifluction) likewise can be found within and without the glacial boundary. Such features are the result of deep seasonal freeze and thaw. Differences in topography, or the configuration of slopes, such as may be seen at different distances from the drift border, give clues to probable climatic differences of glacial time (69). Where there is evidence of cryoplanation, i.e., the process of molding the landscape by frost action, there must have been fairly severe frost action. The plant geographer is particularly concerned with the question as to how far outside the glacial boundary and at what altitudes features arising from severe frost action occur.

Periglacial frost phenomena (block concentrations, block cascades, etc.) have been described in the eastern part of the Driftless Area at latitude 43° N., within 10–20 miles of the Wisconsin glacial boundary. These are interpreted as indicating that, for at least a part of Wisconsin time, the climate of the Driftless area was more rigorous than at present and had some similarity to that now found in subarctic regions (178). Periglacial block streams have been found along the northern Blue Ridge from southern Pennsylvania to northern West Virginia (latitude 39°–40°) (179, 180).

It is believed that a "surficial deposit and the associated landscapes in the periglacial area, or area within a few tens of miles of the Wisconsin drift border [on the high Appalachian Plateau of northcentral Pennsylvania] are the result of processes caused by the adjacent Wisconsin ice sheet" (69). Topographic contrasts can be seen in a traverse from the drift border southwestward for about 75 miles (latitude ca. 40°–41°). Near the drift border "the evidence is good that in favorable localities the present frost climate is sufficient to maintain a miniature blockfield or to produce miniature boulder rings if the vegetation is removed" (69). All of these features are said to indicate that frost action in the periglacial belt in northcentral Pennsylvania was more intense than

at present, and that the annual depth of frost penetration was as much as six feet and somewhat greater than at present. It is a known fact that winter temperatures of soil beneath a vegetation cover and of soil not so covered are very different (for data, see 215).

Blockfields and thick surficial deposits occur in the higher parts of the Appalachians as far south as the Great Smoky Mountains (69). In the Great Smoky Mountains frost phenomena give evidence that there was a timber-line, probably in the last cold phase of the Pleistocene, at an elevation between 4000 and 5000 feet (120), which would mean a lowering of altitudinal belts of about 2000 feet. As these mountains rise from elevations of about 1000–1200 feet, there was still ample altitudinal range for the several forest zones now represented on the slopes, and habitats sufficiently similar to permit the necessary downward and upward migrations of species.

Additional physical features which may give some idea of glacial climates are outlined by Flint (87). Of these, evidence of chilling of sea water and of the formation of sea ice are of value in suggesting possible coastal conditions. " Studies indicate that there was general cooling of the water in middle and low latitudes ", the amount of cooling varying from place to place (144). Although the broad features of oceanic circulation were probably similar to the present circulation, there were important differences. Cold water extended farther south than at present, as indicated by the finding of ice-rafted pebbles in the western North Atlantic as far south at latitude 40° N., and " possibly pack ice extended as far south as 40° N. Lat.". This affected the Gulf Stream, and " it is doubtful whether the northern edge of the Gulf Stream system reached a latitude much higher than that of Cape Hatteras " (144). As a result it is probable that coastal areas of eastern United States were colder than at present, at least as far south as North Carolina, and possible that fogs were frequent toward the southern limit of the cold air mass overlying the cold drift.

Pleistocene fossils give good evidence of climatic conditions, provided the plants grew in the area where the deposit is found, and that their physiological requirements and tolerance ranges were the same as those of modern biotypes of the species represented. " Most widespread and common plant species consist of a

large number of genetically different biotypes, many of which differ widely in their ecological preferences. This is . . . the basis of the ecotype concept, which conceives of these widespread species as consisting of several clusters of similar biotypes, each cluster, or ecotype differing from other ecotypes in its ecological preferences" (183). White spruce, black spruce, balsam fir, jack pine, and other common and widespread species are ones commonly emphasized as indicative of climatic conditions in which their ecotypes in the North are now growing. There may have been other ecotypes in the past, just as there have been other species (cf. South Carolina buried soils), and these cannot be identified by plant fragments and pollen grains. It is not suggested that the ecological requirements were greatly different, but they may have been at one extreme of the tolerance range as manifested today.

A few deposits are selected to illustrate possible significance of fossils in Pleistocene deposits.

The Two Creeks forest bed in eastern Wisconsin (211, 212) is of particular interest because it gives evidence of conditions at the edge of an ice sheet, but not one of those which forms part of the glacial boundary. A spruce forest established itself on the lake flats exposed when the waters of the Glenwood stage of Lake Chicago fell to below the present level of Lake Michigan; this was when the Cary ice-front was somewhere north of the Straits of Mackinac. Readvance of the ice (of the Mankato substage) ponded the water throughout the forest, and silt was sifted between the upright moss plants which were buried alive (chloroplasts remain). Then the area was overridden by ice (Mankato) and trees were pushed over. The forest had been thriving for at least 62 years before the gradual decrease in width of growth rings began 20 years before the forest was destroyed. The majority of the logs point in a southwest-northeast direction (the advance of ice was from the northeast), and "one log, seven feet long, was found partly attached to its stump, and leaning at an angle of forty-five degrees . . . . About three feet of sedimentary deposit accumulated before the ice reached the spot. When the ice did override the area it apparently pushed this tree over to an angle of forty-five degrees in the soft mud and sand. Then it tore off the portion which protruded from the sediments leaving a shredded and twisted end to the log. This shredded character of the wood

is indicative of live or very recently killed timber" (212). Although spruce forest is a northern type, its persistence at the very margin of the ice at latitude 44° N. is significant. Wilson has found that *Picea* rapidly invaded newly exposed soil, but that this forest zone was only a few miles wide. It is only reasonable to assume that at lower latitudes the climatic effects of proximity of ice would be somewhat less.

A late Pleistocene deposit in Minneapolis contains the remains of species which grew in a bog forest (larch, black spruce) and in a climax forest (white spruce, fir, white pine, paper birch) at a time when the retreating ice front "was certainly not more than 150 miles distant and probably very much closer" (55). While the bog forest type still lingers nearby, "the conifer forest which once inhabited the uplands, has been entirely superseded, here and for a hundred miles northward, by oaks, maples and other deciduous trees" (57). Evidently, forest displacement even at latitude 45° N. was not extreme.

If the plant remains of the Little Bayou Sara deposit in Louisiana—where "the remains of typically northern species" have been found with those of southern species (see "Pleistocene History" and 35)—are of early Sangamon time, as has been suggested (67), they date from a time of waning of the Illinoian ice sheet which had been sending meltwater into the Mississippi River some 600–700 miles to the north (more if all the meanders are included). Climatic conditions had not been severe enough to displace *Taxodium* (stumps in situ); spruce is an early invader of newly exposed soil, and cones floating down the river could have supplied seed. The uneroded condition of a spruce cone in the deposit is given as evidence that it was not transported any great distance. Cooler summers than now, with more fogginess which might easily result from the nearness of cold water, may explain the mixture, which does not indicate displacement of the sort of vegetation now prevalent in the latitude.

Some buried soils of Pleistocene age (probably early Pleistocene) near Spartanburg, S. C., contain an interesting assortment of pollens. A reconstruction of the vegetation of the area during the time of sedimentation would be: "The rolling uplands were covered by a climax of oak-hickory-chestnut; ravines and protected slopes contained stands of mixed mesophytes; several places where

small streams were impounded postclimax spruce-fir grew on and around bog-like basins; over the upland the prevailing climax was interrupted by stands of pine and pine-hardwood mixtures" (39). A significant fact is that "the *Abies* is not one of the modern species of Eastern America"; it may be an extinct species. Can it be possible that this is evidence that ancestral fir, and perhaps spruce, had been in the East since the time of the early (Mesozoic) records? As an explanation of the spruce-fir community in the vegetation pattern of the Spartanburg area, the possibility of pronounced frost pockets suggests itself. Near Petersham, Mass., at an elevation of 1100 feet on the Harvard Forest, red spruce occupies a frost pocket where temperatures 22° F. below those of the surrounding deciduous woodland are recorded; on Mt. Monadnock, only 25–30 miles to the north, the spruce zone begins at an elevation of about 2300 feet.

The North Carolina pollen profiles (see Pollen Record) indicating climates during glacial ages and subages considerably cooler than the present, seem to reflect the influence of colder ocean waters and perhaps fog. This pollen evidence of the southward penetration of cooler climate vegetation on the Coastal Plain is in accord with the map showing "the effect of introgression in forming geographic subspecies within *Juniperus virginiana*"; the northern race extends southward on the Atlantic slope to about South Carolina (9).

How much lowering of temperature was necessary to bring about the various features noted? No estimates are available except those based on lowering of regional snow lines in mountains, where the calculated reduction in mean temperatures range from 4° to 7° or 8° C. in different mountain areas, the highest being for western Europe, Italy and Greece (87). Other statements are comparative only. Reviewing the probable effects of climate on vegetation south of the ice margin, it appears that "the margin of a glacier is held stationary or recedes because wasting equals or exceeds the rate of ice advance" and that "during wasting, surfaces become covered with detritus which . . . may temporarily insulate the frozen mass within". Thus the marginal band of the glacier would be little different from a perennially frozen soil band in its temperature effects on adjacent areas. Also, atmospheric circulation was affected because of the permanent high-

pressure areas developing over ice-caps; the thermal gradient south of the ice was increased, and hence storminess increased (33).

What were the effects on vegetation? Opinions differ greatly, ranging from those of Deevey who proposed the "hypothesis of Pleistocene origin of existing distribution patterns" and suggested that "the typical temperate species were pushed south of the Rio Grande and deep into peninsular Florida", to those of other authors who maintain that it seems entirely possible that some temperate species may have persisted at or near the ice margin and that displacement amounted to a narrowing of the deciduous forest belt at the north and lowering of its altitudinal range in the mountains. It is doubtful that deciduous forest ever could have occupied any considerable area on the Coastal Plain where soils, except in local areas on river bluffs, are unsuitable. As Cain has suggested (38), "much of the whole region south of the terminal moraine provided territory for preservation, but the centers were generally the regions of varied topography and conditions (the Southern Appalachians and Cumberlands, the Ozark plateau, etc.)".

It must be remembered that glaciation was not a single event, that the hypothesis that temperate species were "pushed" far south must assume that similar migrations took place not once but during each cold phase of the Pleistocene—in Nebraskan, Kansan, Illinoian, and Wisconsin time—with some to and fro movements in the glacial subages. If "the warmth-loving species, including many or perhaps most of the 'Miocene relicts', survived in peninsular Florida and in Mexico, and have subsequently migrated to their present localities", the migrations of Wisconsin and post-Wisconsin time were not the only ones. In other words, these temperate species, whose ranges are so simply explained by an hypothesis of persistence, must have gone to Mexico or Florida at least four times, only to return and assume a pattern of distribution in favorable habitats related to Tertiary physiographic history. Yet no evidence has been left behind in these remote areas, either in the fossil record or in the form of isolated occurrence of temperate species of restricted range; the Mexican occurrence of species of wide range and low rates of evolution, as *Liquidambar styraciflua, Mitchella repens* or the subspecies of

Fagus, is more easily explained by disruption of range because of late Tertiary aridity than by Pleistocene migration. Could any considerable population of mesophytes of rich humus soil find edaphically suitable areas on the Coastal Plain in which to survive while in peninsular Florida, or to occupy while migrating to and from Mexico?

It is suggested that the coastal plain disjuncts on the Appalachian Upland may have taken part in these migrations, "some of them perhaps having been driven into Mexico and peninsular Florida" (66). If these disjuncts arrived by post-Wisconsin migration from Florida and Mexico, or even from the Gulf and South Atlantic Coastal Plain, how can the relationships displayed by *Asclepias, Sarracenia,* etc., be explained? Can such distinct specific differentiation as is apparent between upland and coastal plain species of *Conradina* be ascribed to the last few thousand years? Is it possible that migrations from upland to coastal plain and back again took place four times, each move involving the spanning of wide edaphic barriers?

The edaphic requirements of species could not have changed radically each time that temperatures were lowered, at least not enough to have permitted the many species of exacting requirements (which are the ones of local or restricted distribution) to move hundreds of miles across lands offering few if any suitable habitats. If such migrations took place, they must have been initiated not by low temperatures prevalent at the time of maximum development of an ice sheet, but during the gradual lowering accompanying advance of ice sheets. Yet we know from the evidence of the Two-Creeks forest bed that there a forest stayed until actually overwhelmed by ice. Also, the return migration could not have been delayed until the onset of unfavorable temperatures in the area of refuge, for by that time the intervening area would have been impassable, if it were not always so. Moreover, the temperature tolerance range of most species is considerably more than that to which they are naturally subjected, except at the limits of range. For example, *Shortia galacifolia* is hardy in Quebec and New Hampshire (116); *Rhododendron catawbiense* in northern New York State; *Rhododendron carolinianum* in Norfolk, Connecticut, where hundreds of plants have established themselves from self-sown seed, and during which time a temperature of –27° F. was recorded (89); *Neviusia alabamensis*

shows no effects of temperatures of –13° F; *Magnolia tripetala* can be grown in Minneapolis. These "Miocene relicts" are hardly "warmth-loving".

Against such an hypothesis of extreme southward migration, of the shaping of distribution patterns by Pleistocene glaciation, and of Pleistocene speciation and subspeciation of most taxa, we must weigh the known stability of many of our tree species and the inferred stability of others (low rate of evolution indicated by close relation of American and Asiatic species), the relative positions of diploid and tetraploid races of some species, the patterns of introgression, the tolerance range (temperature, soil, length of day, etc.), the distribution patterns of a great many species. We must recognize moderate shifts in range, shifts which would permit such xero-mesophytes as the species of *Cercis* to come into contact, shifts which would modify or determine northern limits of range, and of course the several easily demonstrable shifts of late-glacial and postglacial times. We must look for regional, not general, climatic influences which can explain changes in coastal plain vegetation indicated by pollen diagrams. We must keep biotype variability in mind.

The many facts considered under the headings "Floristics" and "Contributing Fields of Botany" must be weighed, along with those derived from known physical effects of glaciation, the fossil record, and physiographic history of unglaciated eastern United States, in arriving at a reasonable interpretation of the intricate but consistent pattern of distribution.

Evidence indicates that in many instances the "historical factors" determine the physiographic area in which a species occurs; the climatic factors of the recent past and the present determine the geographic limits; the edaphic factors determine the precise area occupied within the limits of the larger areas determined by past events and present and past climates.

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